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TRANSACTIONS OF THE ROYAL SOCIETY OF CANADA

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SECTION FIVE



PRESIDENTIAL ADDRESS

Levels of Analysis and Problems of Concept-Formation
in Cytology

C. LEONARD HUSKINS, F.R.S.C.

"Science is an interconnecting group of concepts and conceptual schemes arising out of experiment and observation, and fruitful of new experiments and observations."

IF one accepts this statement by J. B. Conant as a satisfactory brief definition of the type of activity that all of us here are engaged in, it may be of interest to inquire how some of the concepts of cytology, my special field, have developed in the past and are now developing. I think this inquiry will also reveal some of the changing ways of concept-formation that now characterize biology as a whole as it moves from its early descriptive stages to its present development in which it is in many phases linking up with chemistry and physics. Since our interests within biology and medicine are so diversified and every one of our fields is today very highly specialized, I shall take the liberty of sacrificing detail in favour of clarity through generalization, though I shall, of course, try to avoid distortion in the process.

We may roughly divide the history of cytology into three stages. We then find, in brief, that in the earliest period when the concepts were *thought* to come from direct observation of tissues and cells, they probably were influenced by extraneous ideas much more than was realized. Of course what we see is always determined by the previous experiences of our central nervous system; the difference is that we realize this more clearly than did most of our scientific forbears, partly because they thought their efforts were revealing Reality—with a capital R. In the second phase the concepts of cytology were greatly influenced by genetics; the relation was reciprocal and the hybrid science of cytogenetics developed rapidly. In the current stage of cytology the most exciting concepts, as in genetics, are embodying data and ideas from physics and chemistry; we are all striving as best we can to think in terms of function, that is really to become developmental physiologists. Of course any subdivision or classification of any

science (or of anything) is to some extent arbitrary and at all stages there are, and must be, interactions between all sorts of ideas and all sorts of data. But it seems that to comprehend we must first subdivide and classify; the completeness or incompleteness of the synthesis (the view of the whole) that we make at any stage in the progress of our understanding, is in direct relation to our understanding of the parts, though it is always more than this.

Cytology began with the invention of the microscope. This followed the development of the telescope and I believe that many of the early errors of descriptive cytology arose from failure to recognize that at the terrestrial level these two instruments do two entirely different jobs. A spy glass, or a pair of field glasses, brings the distant but familiar into nearby focus; the microscope revealed a world new to our senses; the electron microscope is today revealing a still newer "submicroscopic" world which we have hitherto conceptualized chiefly from indirect evidence. To understand a new world we have perforce, as in all learning, to put the unfamiliar in terms of the familiar; Hooke's initial use of the word "cell" is an all too obvious example. How else can one explain the persistence for nearly a hundred years of the concept of amitosis or direct cell division other than as a transfer of the earlier observation that protozoa and bacteria "multiply by fission."

Let us examine some stages in the development and decline of this concept that cells divide merely by direct fission. The division of cells was probably first observed by Prevost and Dumas in 1824, but they did not realize its significance. Fourteen years later Schleiden and Schwann demonstrated the (almost) universality of cells. Their concepts of cellular reproduction, or rather production, provided, in general, that the new cells crystallized out of the nutritive substance or embryonic protoplasm. Considering how clearly cell division can be seen with even the simplest compound microscope, it seems that ideas derived either from crystallography or from creation mythologies (cf. the "Urschleim" concepts of the origin of life), or both, must have determined that, to us absurd, concept. Within a few years not only had it been demonstrated that cells arise by division but it had been shown that nuclear division precedes cell division. By 1848 Hofmeister had seen chromosomes. This later development may have been made possible by the development of the achromatic objective, which occurred between 1815 and 1830, but according to Hughes (1952), Fresnel in 1824 found that the contemporary achromatic microscope had no advantages over the earlier uncorrected objective at magnifications greater than 200x and Sachs records that as late as 1836 Meyen

still preferred an English eighteenth-century instrument. Hooke, Leeuwenhoek, Grew, and Malpighi, we may recall, made their great discoveries late in the seventeenth century! Incidentally, if Schleiden and Schwann were wrongly influenced by primitive concepts, theirs is one of the few cases in cytology; it seems today that the ideas of Plato, once sophisticated, have been responsible for many more of the misconceptions modern biology has slowly discarded (or is still be-devilled by).

By 1855 cell division was recognized as the only method for cell reproduction and in that year Remak, studying blood cells in the chick embryo, pictured first a splitting of the nucleolus, next a splitting of the nucleus, then a division of the cytosome, then of the entire cell body, and finally of the cell membrane. He evidently had a passion for consistency! For nearly twenty years some such method of "direct nuclear division" was the only kind considered possible, but by 1876, after the invention of the oil-immersion objective, so-called "indirect division," i.e., mitosis, was considered equally important. In 1882 Flemming stated that mitosis was the almost universal process and that "direct division" or amitosis was very rare. But in the same year Strasburger claimed that both mitosis and amitosis were normal and that the mitosis occurring in higher forms was derived from the amitotic type which, he thought, still occurred in lower forms. In 1891 Flemming effectively disposed of Strasburger's argument by publication of *observations*. But more important for our analysis of concept-formation is the fact that the concept of amitosis as a mechanism for normal nuclear reproduction had been rendered virtually untenable in 1888 by Roux's critical analysis of the issue. He pointed out that mitosis is a complex process obviously requiring much energy as well as time; it must therefore have had a high selective value if it has replaced the much simpler mechanism of amitosis. The basis for this he thought obvious: mitosis provides a mechanism for qualitative as well as quantitative division, whereas amitosis would be effective only if the materials to be divided were undifferentiated granules. Amitosis survived in the text-books, however, for more than half a century longer; Kater reported as recently as 1940 that "disagreement is still rampant." Amitotic division probably does occur in degenerating nuclei and one can always see what look like direct divisions in some nuclei of normal tissues; but to accept these as evidence of amitosis as a normal process of nuclear division means that only a dozen years ago there were some biologists whose trust in the evidence of their eyes exceeded their trust in logical analysis of numerous diverse but very relevant data. Had they been consistent they would have believed

the evidence of their eyes that the sun daily moves across the sky!

The concept of the continuous spireme, the idea that at the beginning of mitosis there is in the nucleus a continuous thread-like structure that breaks up and forms the chromosomes, has a very curious history. It apparently began with Flemming's earliest work—1879—in which he was more interested in the thread-like nature of the nuclear material than in the number of threads present. He did not pronounce a law of the continuous spireme; he merely assumed it as the apparently simpler concept in the absence of critical evidence that it was discontinuous. He observed that the threads were double very early in the prophase of mitosis and probably sensed that this provided the initial step in a mechanism for the production of two identical sets of longitudinally differentiated chromosomes to be separated into two nuclei, as explicitly formulated in 1883 by Roux. But Strasburger in 1884 was convinced that the thread was continuous, which led Rabl to say the following year: "To date all research on cell division is permeated by a concept which appears to be almost a hereditary sin. It is the supposition that in the beginning of the thread-ball formation a continuously wound thread travels through the entire nucleus. . . ." He reported that "although it is often possible to follow a single thread for some distance . . . with great patience one will regularly come to a point where . . . several threads fuse or the thread actually comes to an end." Then he asks: "Why should one think that the finding of one thread rather than several threads is something better, something more histological?" (We may add that the use and abuse of "Occam's Razor" is still a serious problem in cytology.) Three years later Strasburger abandoned the idea of the continuous spireme and attributed his earlier error to poor fixation. The argument, however, continued unabated for another thirty years. By that time it had got thoroughly confused with the problem of chromosome pairing in meiosis. Somewhere along the line the idea had arisen that in meiosis the chromosomes are initially associated only at their ends (possibly because the continuous spireme broke up only between each of the pairs of chromosomes instead of at every chromosome end) and that only later do they come to lie side by side. The chains of chromosomes found at metaphase in some species of *Oenothera* were thought to confirm this concept of end to end (telosynaptic) pairing. A much more complicated, and now well-established, explanation of the *Oenothera* case, for which the data were derived about equally from genetics and cytology, finally disposed of both telosynapsis and the continuous spireme concepts. How either of them came to be so widely accepted when all along there had been good descriptive evidence for the al-

ternative view that the thread is discontinuous and that pairing is side by side, with the end to end arrangement secondary when it occurs at all, is hard to understand, especially since these alternative direct observations could be, and quite early were, logically correlated with developmental and genetic data and concepts. It sometimes seems that those cytologists who "refused to theorize," who stressed the value of direct visual evidence over that of indirect evidence from other fields, actually were subconsciously prejudiced against indirect evidence and therefore gave it a negative value. The situation has changed, and perhaps has gone to the other extreme, since about 1930!

That the thread-like structures of prophase form spirals which determine the sausage-like shape of the metaphase chromosomes of meiosis was seen by Baranetsky in 1880. Strasburger could not see the helix within the metaphase chromosome, and apparently only two cytologists, Vajdovsky and Bonnevie, did so (or had the nerve to say emphatically that they did) in the next forty-five years. This is not to minimize the greatness of Strasburger. Because the essential nature of scientific understanding is progressive and human nature is commonly conservative, the degree to which a scientist's ideas may be correlated with delayed formation of new concepts by his followers is one indication of his greatness. Since 1925 everybody has seen spiral structure; the concepts concerning its formation and the details of its form in mitosis and meiosis are another matter. Suffice to say here that the most complete unified theory has the largest microscopically-visible spiral depending for its formation on the existence of a smaller spiral which is at the limit of microscopic resolution, and which depends, in turn, on the spiral structure concept of protein molecules. It happens, however, that before this unified concept was formulated, analysis of the changes of direction in the spiral that can clearly be seen had effectively ruled out any such *direct* relationship between molecular spirals and the visible spirals. This was "the new cytology" of the 1930's: a logical theory was better than direct observations—observations that did not fit a logical theory were discredited. It was the earlier pattern in reverse!

From the formulation of deductively derived concepts that integrated cytological and genetic data in the 1930's came some enormous advances. But Schrader (1948) and Sturtevant (1951) have also indicated how unsound in detail were some of the hypotheses that have nevertheless done so much to unify thought and particularly to facilitate teaching in cytogenetics. I will here touch on only one other concept of this period, the one in which the basic error has been recognized by Darlington who propounded it and which has significance

because its abandonment exemplifies what is, I think, undoubtedly a trend towards more complex concepts in both genetics and cytology. Some of these concepts are bound to be better than the earlier simpler ones; if some are erroneous they can hardly be more so than some of those derived from direct observations.

In 1903 Sutton had demonstrated clearly that the segregation of Mendelian genes parallels the segregation of the chromosomes during meiosis. The linear order of the genes on the chromosomes was gradually established and received final confirmation in 1935. This completed the proof that the four chromatids of a pair of conjugated meiotic chromosomes carry (or are) the four strings of Mendelian genes that are distributed to the four nuclei that are produced by the two divisions comprising meiosis. The corollary was that the Mendelian genes being the units of heredity, the chromatid must be, transversely, a unitary structure. But by that date many cytologists had reached the conclusion, from direct observations, especially of large chromosomes, that the chromatid is a two-, four-, or indefinitely multiple-stranded structure. The "precocity theory" which served so nicely both to embrace Mendelism and to "explain" the mechanism of meiosis itself rested on the idea that the chromatid was a single strand. To save the theory it was therefore necessary to claim that the observations of double or quadruple strands in a chromatid must be optical illusions or else that the chromatid, though morphologically a double structure, must be "physiologically" or "effectively" single. For twenty years the theory was "saved" by the first method. X-ray breakage data were predominantly used to *prove* that the observations of doubleness or quadrupleness must be erroneous. X-rays often break both chromatids of a chromosome, sometimes only one, and only relatively rarely cause the cytological or genetic effects that would be expected from half or quarter chromatid breaks. But actually such effects do occur and in up to 20 per cent of cases in some experiments! At first these were ignored; then they were explained away as delayed or secondary effects of the irradiation; finally, it was generally agreed that X-ray bombardment is too crude a method to settle the issue. Its use is analogous to the use of shrapnel when the need is for a precision rifle that will enable only one of two paired targets to be hit. Today the morphological multiplicity of strands in the chromatid is recognized by practically all cytologists and the concept of physiological singleness appears to be both unnecessary and at variance with some cytological evidence. Another obvious possible resolution of the conflict between the cytological and the genetic data seems to be gaining ground though it is not yet widely accepted: this is a change in the concept of the

gene. At the level of ordinary Mendelian analysis the gene is a unit; at the level of the light microscope its carrier, the chromatid, is a double or quadruple structure, at the electron microscopic or the molecular level both may be multiple. That a multiple structure can be a unit in heredity is not too difficult to imagine; how it can be a unit in mutability (which is generally assumed but by no means proved) is a problem for the solution of which we have as yet no very promising suggestions (I have elsewhere, 1947, considered one). Perhaps we shall have to wait for further data on the structure of nucleoproteins. Certainly we shall have to await clarification of our concept of the gene; as I pointed out in our Symposium of two years ago (1950) this has long been more complex and less definite than is commonly recognized—Goldschmidt and McClintock are currently presenting crucial data that demand new concepts of the mutation process and of the nature of the gene. The "aperiodic crystal" as Schrödinger calls it, may help in forming new concepts of the gene and chromosome, though it seems hardly likely to be the all-embracing answer to the problem of "What is Life." Incidentally, *that* book reveals the need for more critical transfer of cytogenetic data by physicists who formulate biophysical concepts.

To conclude these remarks on the second period of cytology: whatever we may teach in elementary cytogenetics we shall not, at the research level, go back to over-simple reliance on direct observations. The electron microscope will provide direct evidence for or against some of our concepts of structure, but using it we shall have to remember that once again a new, unfamiliar world is opening up to our eyes and that it may be quite a long time before our interpretation of what we see in electron micrographs can be relied upon.

In our current, third phase it is becoming increasingly recognized that Mendel's great contribution to biology was not Mendelian ratios (they even misled in some important aspects) but the concept that heredity depends upon the transmission of differentiated material particles present in the nuclei of reproductive cells. As soon as this was fully established, old notions such as telogony, maternal impressions, and the inheritance of acquired characteristics became logically obsolete. They survive, particularly in Lysenko's brand of Soviet genetics, only because the basic principles of Mendelian inheritance either are not understood or are deliberately ignored (as was the double or multiple structure of the chromatid by most Western geneticists for at least a dozen years after it was sufficiently established). The particulate concept of matter in general goes back, of course, to Democritus (who was so hated by Plato that he wished all his books

burnt). In biology it found definite formulation in Darwin's short-lived "provisional Hypothesis of Pangenesis" and in Mendel's now well-established laws. It is now linking cytology with chemistry and physics. We are lucky that we do not feel it necessary to consider the problem which it posed for scholastic logic. The dilemma to a scholastic philosopher is, as outlined by Herbert Spencer, that if matter can be divided into ever smaller particles then there must be an infinite number of particles and the human mind apparently cannot conceive infinity. On the other hand, if a particle cannot be further divided it cannot be represented, for every model of a particle must have three dimensions and therefore be capable of further division. We shall, of course, be happy if we can analyse living matter down to molecular "particles." The concept of levels of integration enables us to think in terms of diverse levels of unity. This philosophical digression is not, however, irrelevant; it is surprising how over-simplified the concepts of good descriptive cytologists can sometimes be; for instance, at a much higher level, particles that are at the limit of microscopic resolution have often been described as spherical, the fact that at that level particles of any shape will appear spherical, though well known, having apparently been overlooked. There are biologists who still think of protoplasm as composed of undifferentiated particles—not consciously, of course, but evidently unconsciously, since this thinking is inherent in some of the concepts they still accept. The logical paradox that Spencer cited will not bother us because we know (a) the limitations of our ordinary three-dimensional models at the molecular and atomic levels, and (b) that while indefinitely continued division is logically possible for undifferentiated matter there are definite limits to the subdivision of any structurally differentiated material. Structure is fundamental in our general thinking; it is, as Frey-Wyssling makes clear, structure that is the fundamental feature of living matter—as we see the problem today. It is, to me, a startling fact that different structural arrangements and/or proportions of carbon, hydrogen, oxygen and nitrogen atoms are so largely responsible for the specificities of inconceivably vast numbers of proteins—specificities so significant they may determine life or death for an organism, as in antigen-antibody reactions. In the face of such facts as this, Aristotelian reasonings on form and matter become equivalent to a child's play with Tinker Toys and Hegelian or Marxian transformations of quantity into quality appear as the dawn of adolescent understanding.

Before going on to concept-forming in the current phase of cytology we might stop to consider the steps involved in the formation and breakdown of the law of constancy of chromosome numbers, since this

process extends across all three stages. In brief it seems to have been somewhat like this: (1) the nucleus was found to be composed of chromosomes during the division cycle, but these were not observable during the resting stage; (2) they were therefore formed either from a network of chromatin or from a continuous spireme thread; (3) the number was found to be more or less constant; (4) genetic data seemed to require constancy of the genetic constitution of all cells produced by mitosis and the concept which related Mendelian genes to the chromosomes therefore demanded that the chromosome constitution be the same in all cells that are produced by mitosis; (5) genetic data demanded the maintenance of chromosome individuality during the resting stage when they could not be seen; (6) exceptional observations of deviant chromosome numbers were therefore attributed to error or the deviating numbers were assumed to be abnormal or the result of wounding or other pathological conditions; (7) once the chromosome theory of heredity was firmly established it was natural for everyone to begin looking for exceptions to it and the breakdown of the constancy concept began; (8) then it was recognized that both the cytological and the genetic methods of determining chromosome numbers were too crude—both could give an answer only for cells that were reproducing themselves; (9) indirect determination of chromosome number by the counting of heterochromatic chromosomes or parts of chromosomes that were observable in non-dividing cells revealed that high multiple numbers were often present, as had been predicted earlier from the occurrence of progressive size classes of nuclei; (10) stimulation to division, by means of auxins or wounding, of nuclei that ordinarily would not have divided again showed multiple chromosome numbers; (11) the concept of constancy of chromosome number is today recognized to be strictly limited, perhaps especially to germ cells and embryonic or meristematic tissues as Winkler, almost alone, had indicated in 1916, two years before the constancy concept was formulated as a "law." It may be added as a 12th point (developed later herein) that in the current third phase the chromosome content of nuclei is being estimated from the desoxyribose nucleic acid content as determined by photometric absorption techniques. Until very recently this could be done only in more or less homogeneous "resting" nuclei. A new technique developed independently by Ornstein at Columbia and by my colleague, Klaus Patau, now permits measurement of DNA in nuclei at any stage and even in individual chromosomes.

Leaving the chromosomes as such for the moment, but before passing on to the cytoplasm in general, we might list in passing the chief con-

cepts of spindle formation. From direct observation there are concepts of fibres pulling or contracting, or of other fibres growing and pushing, of the whole spindle expanding, of streaming and diffusion, and so on. From colloid chemistry there are concepts involving viscosity and hydration. Electrostatic models have been made—the most comprehensive one to date seems far too simple. Consideration of hydrodynamic forces has led to concepts of which Schrader (1944) says some have "some potential value" but for which "some factual support is very badly needed." Interionic forces that produce tactoids are among the most recent ideas, but they have not yet led far. The biggest complication for any theory is that there appears to be chromosome autonomy in movement as well as chromosome submission to being moved by the spindle.

For the cytoplasm in general we have had many concepts. The original description of it by Dujardin in 1835 was: "a gelatinous substance, perfectly homogeneous, elastic, contractile, diaphanous, insoluble in water and without traces of organization"; from this we proceeded through the micellar concept of Nägeli, the reticulate, the alveolar, the emulsoid, the granular, the colloidal, and now back to a micellar concept that utilizes concepts of structural chemistry to explain the submicroscopically determined fibrils or micellæ. It was, I think, the "telescope error" that caused neglect of Nägeli's early micellar concept. "What holds the micelles together?" some cytologists asked, thinking in terms of bricks and mortar and neglecting to think of "forces" that come into play at submicroscopic dimensions.

This leads us to the next and final topic of this paper—the development of concepts of the physico-chemical composition of the chromosome. Unfortunately, the data that have to be encompassed are already so diversified and numerous that only the high lights of the issues involved can be touched upon. Chemical analyses of sperm heads long ago made it probable that the chromosomes are composed of nucleoproteins; biochemical concepts of the complexity and variety of proteins and the *relative* simplicity of nucleic acids early made it seem likely to most cytogeneticists that the specificity of the genes depended on their protein moiety. It has therefore been somewhat of a surprise to many when during the last few years it has been claimed: (1) that nucleic acids appear to be universally associated with self-reproducing bodies—chromosomes, plastids, mitochondria, centrioles, viruses—and (2) that the protein content of nuclei varies tremendously whereas there appears to be a high degree of constancy in total deoxyribose nucleic acid content. Sperm and pollen nuclei contain half the amount of DNA characteristic of the nuclei of embryonic or

meristematic tissues while nuclei of many older tissues, where mitoses are rare or absent, show the same or some multiple of the amount found in nuclei of embryonic cells. Constancy of DNA per nucleus becomes meaningful if related to chromosome number; most of the evidence (though by no means all) indicates a degree of constancy or replication parallel to that of chromosome number in differentiated tissues. The relationship to the gene (when we have clarified and extended our concepts of it) may be much less simple! Elsewhere (1947) I have argued that for heuristic reasons we should distinguish, at least temporarily, between the gene of heredity and the gene of differentiation and development. This was also proposed by Darlington shortly afterwards. The DNA data seem to me to make this more than ever desirable; if, as seems probable, they give us a reliable method of estimating chromosome number in non-dividing as well as mitotic nuclei, they thereby give us direct evidence on the maintenance and distribution of the genome. That the gene of differentiation, or even the gene of "gene mutation," *sensu stricta*, is the same thing as the gene of simple Mendelian analyses (which is merely a segment of a chromatid) cannot at this time be asserted with any confidence.

Enzymatic digestion analyses of the giant salivary gland chromosomes of Diptera showed a protein framework and a concentration of proteins in the bands, which most cytogeneticists considered the loci of the genes. But when the first measurements of DNA in germ cells undergoing meiosis seemed to show a doubling at the stage when the paired chromosomes become visibly split into the four chromatids, which are the second level units, the gene strings, of Mendelian segregation, it seemed logical to assume that the essential component of a gene must be the nucleic acid. How then account for the extraordinary differentiation and specificity of the genes? The first, apparently easy, way out was, of course, the assumption that nucleic acids must be more complex and of much greater variety than hitherto supposed. Chargaff and others have since provided evidence for this, but so far there is no method of determining differences along the length of the chromosomes.

It is pleasant to record that there has not so far been any serious lining up of workers into two opposed schools on the protein vs. nucleic acid nature of the gene question (the word nucleoprotein itself forces recognition of interaction), nor even on the DNA constancy question, such as it seems probable would have occurred if the attitudes towards concept forming of any period up to about twenty-five years ago were prevailing today. All (or almost all) of us in cytology or genetics today realize that biological concepts have to be complex;

both genetics and cytology have become branches (or roots) of developmental physiology. We have therefore in our current concept-forming to encompass, as far as our training and capacities permit, data from genetics, from descriptive cytology using the apochromatic objective, and the newer phase contrast system, from electron micrographs and radioautographs, from the microspectroscope and various photometric devices for measuring "natural" or specifically stained structures, from use of the ultramicroscope and the polarization microscope, from the chemical analysis of isolated chromosomes and other constituents, from X-ray diffraction images and the effects of diverse radiations, in fact from almost every tool used in any branch of science that deals with the structure and/or transformation of matter. As an example of the use of tools taken from another branch of science: one of my colleagues, R. E. Duncan, is using a technique developed in chemotherapy for the investigation of the effects of certain chemical analogues of some of the important constituents of chromosomes.

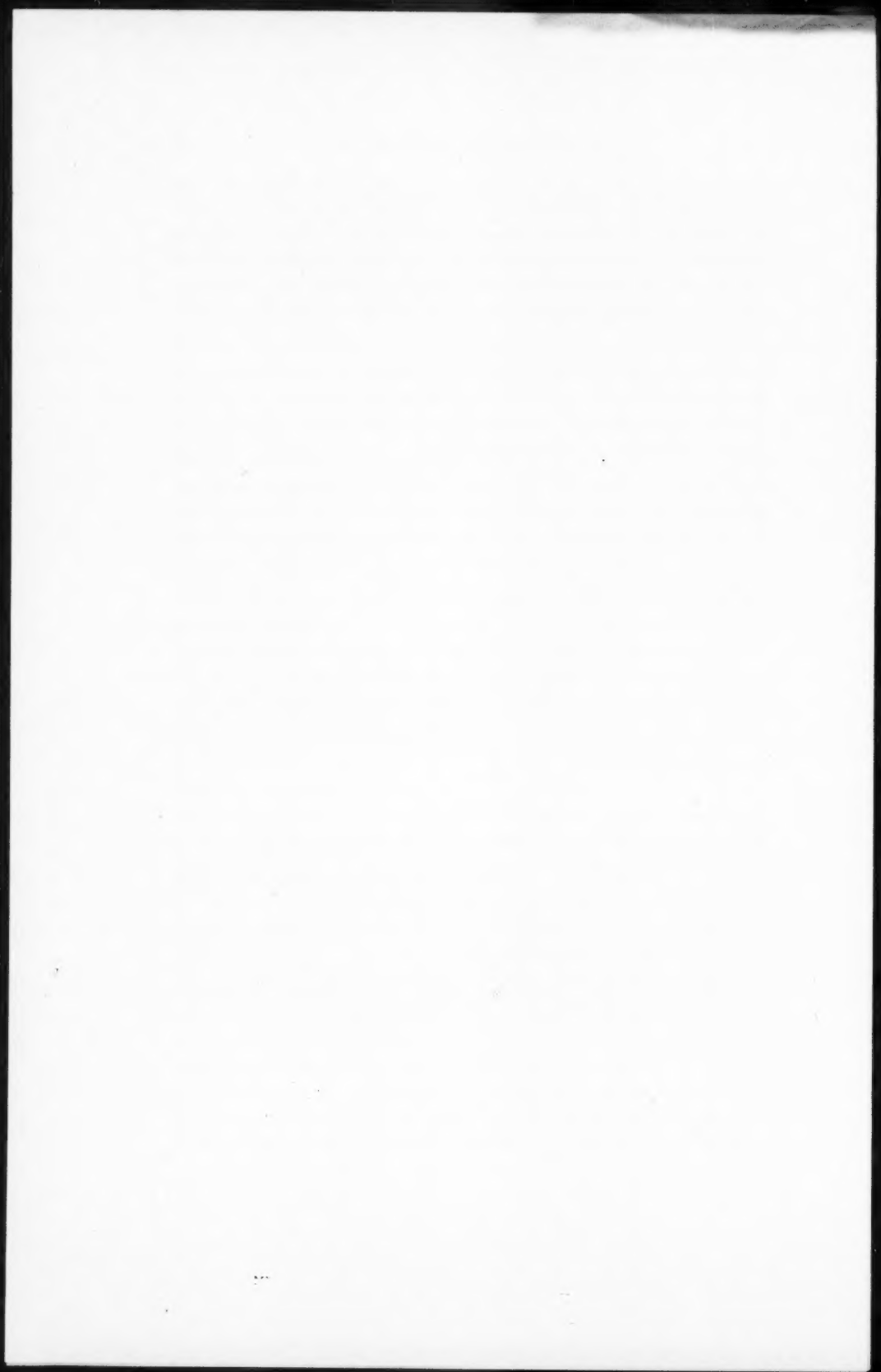
The complexity and the obviously indirect nature of the data that must be used in current concept-formation in cytology in themselves ensure against over-simplification. In addition, all cytologists are today all too well aware that we must not place too much reliance on the direct evidence of our eyes and that all our mental models, such as that of the genes as beads on a string, or our physical models, such as the chromosomes which we construct of pipe-cleaners, plasticine, or rubber tubes, are useful for teaching the facts of segregation and crossing over, but may be grossly misleading if we take them too seriously as representations of what occurs within the living cell. We know that all evidence which we get from our senses is in a fundamental sense indirect and that the sense impressions we receive from the use of new tools and new techniques usually require translation, a process that may take considerable time.

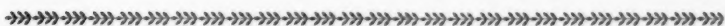
Yet we also know that we can never neglect what we have grown accustomed to call the direct evidence of our eyes. Where we differ from the majority of the early cytologists is in our understanding of the processes of concept- or image-forming. They *knew* that man sees "not with but through the eye," as William Blake expressed it, but they did not always remember it. We are continuously aware that our eyes and the lens system of a microscope are alike components of a compound instrument which functions by transmitting electric impulses to the brain. And the image the brain makes from those impulses is influenced, or perhaps even determined, by the simpler images it has previously constructed from electric impulses received

through the medium of any or all of our sense organs. Thus, through the eye we see chromomeres or bands across the chromosomes throughout their length and these correspond to the image geneticists have formed of gene alignment, which their brains derived from counts of the frequencies of different combinations of macroscopic characteristics. Our satisfaction when the cytological and genetic, the directly and indirectly formed pictures coincide must be similar to that of the structural chemist when X-ray diffraction patterns reveal spacings and arrangements in harmony with the models of atomic spacings he has constructed from his indirect evidence. The question of whether the chromomeres and bands are blobs of nucleoprotein or turns of a spiral is, like the problems of atomic structure, a new problem at a different level of integration. We know from such coincident evidence that we can trust our different senses to reveal consistent impressions, that our interpretations have reality, though they are not revelations of the Reality with a capital R that most of our scientific forbears thought it was the job of science to uncover. For our greater comprehension in this regard we are, I think, above all indebted to the physicists and physical chemists who in turn owe much to the mathematicians and to those analysts of the nature of science and scientific concepts who, within or outside of their own ranks, and whatever their academic labels, are, I believe, the most significant philosophers of the modern world. Through their efforts we are both learning the limitations of human knowledge and gaining the comprehension of, that is the capacity to handle, if not fully to understand, the atom of matter and the gene of life.

REFERENCES

- HUGHES, ARTHUR (1952). The mitotic cycle: The cytoplasm and nucleus during interphase and mitosis. London: Butterworth's Scientific Publications.
- HUSKINS, C. LEONARD (1947). Subdivision of the chromosomes and their multiplications in non-dividing tissues. *Amer. Nat.* **81**: 401-34.
- (1950). Genes. *Proc. Roy. Soc. Can.*, 3rd ser., **44**: 246.
- SCHRADER, FRANZ (1944). Mitosis: The movements of chromosomes in cell division. New York: Columbia University Press.
- (1948). Three quarter-centuries of cytology. *Science* **107**: 155-9.
- STURTEVANT, A. H. (1951). The relation of genes and chromosomes. Chapter 6 of *Genetics in the 20th Century*. New York: Macmillan.





FLAVELLE MEDALLIST'S ADDRESS

The Production of Life in the Bay of Fundy

A. G. HUNTSMAN, F.R.S.C.

OF all the activities of the universe, life is the most complex one of which we have knowledge. Its production requires a great variety of substances and somewhat special conditions. The chief substance required is water, in which such a great variety of chemical activities can readily take place. The chief condition is strong light, which provides energy for the activities. Hence, a thin layer of water, containing a great variety of substances in solution, lying between the air above with its various gaseous substances and the earth below with its various solid substances, and exposed to sunlight coming through the transparent air, seems an ideal location for the production of life. Shallow inlets from the ocean have such characters, and one of these is the Bay of Fundy. Since the ocean has too much of the dissolved substances or salts for many kinds of life, it is an advantage to have the ocean water diluted, as it is in this bay, by water discharged from land, through rivers—water that is relatively pure through having come via the air in distillation from the ocean under the heating effect of sunlight.

It is very difficult to determine at all accurately how much life is produced in any part of the ocean, and yet it is quite evident that there are great differences from place to place in the amounts produced. A square mile of deep water has more space, water, and solutes for production of life than has a square mile of shallow water, but it has no more sunlight, and no more contact with air and earth. Whatever factors may operate, the numbers of animals and the amount of organic matter found on the bottom indicate that the amount of life in the ocean not only does not increase with increasing depth, that is, room for life, but actually decreases and also that, apart from depth, it decreases with distance from shore. That fisheries are never very far from shore seems to reflect this factor in ocean productivity.

The standing crop, that is, the amount of life that can be removed at any time, is not dependable as a criterion of what is being produced, since there may be long-period accumulations of organisms, particularly in cold water. The amount that can be taken out year after year is

the best indication of the productivity of any part of the ocean. In spite of their imperfections, fisheries statistics provide the best picture yet available of comparative productivity. The world production of fish is estimated (FAO, 1950) as being 25 million metric tons. Of this total, 95 per cent is taken in the northern hemisphere, which has much less water but more shore than the southern hemisphere. In the northern hemisphere, most of the fish are taken in the temperate zone. In the Americas, there are practically no fisheries in the arctic zone, and the tropic zone furnishes less than 5 per cent of the total production in the northern hemisphere. The Bay of Fundy lies in the middle of the temperate zone of high fish productivity. An understanding of the mechanism in this bay should show what conditions are required for high production of life in the ocean.

To solve the problem or to understand how life is produced in the sea, one must appreciate how very different that life is from what we know of life on land. In water, little if any effort is required for an animal to remain at any level above the earth. Except in shallow water, the earth below, that is, the sea bottom, is in darkness and cold, with the lifelessness of a winter night, because water gradually extinguishes any light that enters it. For a wakeful life with the activity that light and heat permit, animals must remain near the surface of the water, or must rise toward it during the day if they sink when inactive or asleep at night. With darkness below, with diffuse light above, and with much restricted vision in every direction, each sea animal lives in a very small and simple world. Unable to direct its course over the earth unless close to the bottom, it goes wherever the water circulates, with the modifications that its movements to and from the surface and its swimming here or there horizontally may determine. Differing from plants in being able to seize its food, the animal best sees food that is above and silhouetted against the diffuse light from the sky; and when food is scarce it is only the wanderer that survives. For such life, circulation of the water in which it floats must determine where it will be found by man who lives on land.

THE PROBLEM

How the fisheries of the Bay of Fundy are produced became an important matter in the late 1920's, when it was proposed that the entrances to Passamaquoddy Bay, which is near the mouth of the Bay of Fundy on the border between the province of New Brunswick and the state of Maine, should be dammed to generate power. At those entrances is the focal point of perhaps the most concentrated fishery for locally grown fish that is known, the capture in weirs of herring,

chiefly the small ones for canning as sardines. It was judged that the correlation of this focal point with peculiar hydrographic conditions was significant and that the dams would greatly alter those conditions (Huntsman, 1928). The United States and Canada set up a commission which conducted investigations from 1931 to 1933 to determine the extent of any adverse effects that the dams might be expected to have on the fishery.

The investigators carried out admirable hydrographic, phytoplanktonic, zooplanktonic, and fishery surveys. They were limited to less than two years of field work, which practically precluded more than a testing of any ideas in mind as to adverse effects. Unfortunately there was no background of knowledge of how the fishery is produced. Each specialist looked for a local favourable peculiarity that would be eliminated by the dams. The hydrographer found (Watson, 1936) that the exceptional mixing of water in the entrances to Passamaquoddy Bay, which would be stopped by the dams and which had been claimed as an important factor, forms a small and negligible part of the total mixing throughout the Bay of Fundy. The phytoplanktologists found (Gran and Braarud, 1935) that the mixing is detrimental to plant growth and that the sardine region which would be affected by the dams is quite low in production of the plants to start the food chain leading to fishes. The zooplanktologists found (Fish and Johnson, 1937) that the region is characterized by small volumes of the animals that serve as food for the herring and is relatively unproductive. The ichthyologist could not see (Graham, 1936) that there were necessarily any more herring in the region than elsewhere in the Bay of Fundy and neighbouring Gulf of Maine and considered that the very large quantities caught might merely represent favourable conditions for their capture. This last was an attempt to solve the problem of the greatness of the fishery; but only by casting doubt on the uniform conclusions, drawn from visual observation (herring live near the surface in summer) and from the results of various kinds of fishing, that the fish are exceptionally abundant in the region and that the focal point in their abundance is in the entrances to Passamaquoddy Bay.

The positive results of the investigations revealed no reason why there should be more fish taken there than elsewhere and some reasons why there should be less. This made more of a puzzle than ever of the fact that enormous quantities of fish continue to be taken year after year in the region centred at the entrances to Passamaquoddy Bay. Yet it seemed incontrovertible that very large quantities of herring are grown in the region and become in some places extremely fat in feeding upon planktonic animals that must come from the Gulf of Maine

(Huntsman, 1938). Transport of food for the herring and even of the herring themselves (Huntsman, 1934) was seen as a possible solution of part of the problem.

THE PICTURE

We are able to see a picture clearly when there are distinct contrasts. The Bay of Fundy presents very great contrasts in the quantities of fish produced in its various parts (Fig. 1). The impossibility of making an accurate census of the fish in the sea prevents refutation of any claim that the differences in quantities of fish caught do not reflect differences in local abundance of fish. Nevertheless, critical consideration of facts warrants no other conclusion than that fishery results do reflect differ-

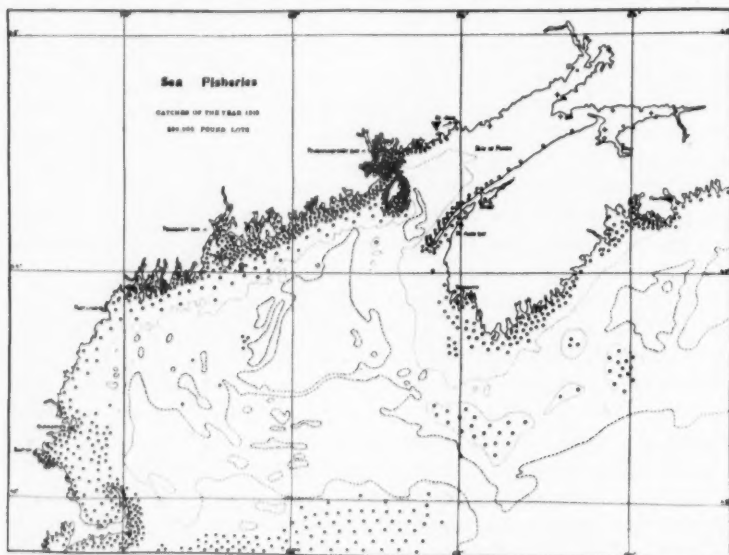


FIGURE 1.—Catches of fish from Cape Cod to Halifax in 1919, each dot representing 500,000 pounds. Bay of Fundy at top on right. Prepared by Dr. A. W. H. Needler.

ences in fish abundance, although not perfectly. In Fig. 2, the waters of the Bay of Fundy have been somewhat arbitrarily divided among the various coastal districts for which fisheries statistics are reported. For each district, the number of pounds per acre is given as calculated from its area and from the amounts of fish landed at the local ports in 1941. Two facts stand out: The very high figure (147) for Charlotte County at the mouth of the bay on the west side, which is the Passama-

quoddy region, and the very low figures (0.05 to 2.2) for the extensive inlets connected with the head of the bay. It will also be seen that the lowest figures (0.05 and 0.3) are at the head of the bay since there are somewhat higher ones (1.6 and 2.2) at the heads of the inlets. Another feature is that the figures for the New Brunswick shore of the bay are higher at the mouth and lower at the head than those on the Nova Scotian shore. Study has shown that these differences occur regularly. They constitute the picture, for which the causal background is to be elucidated.

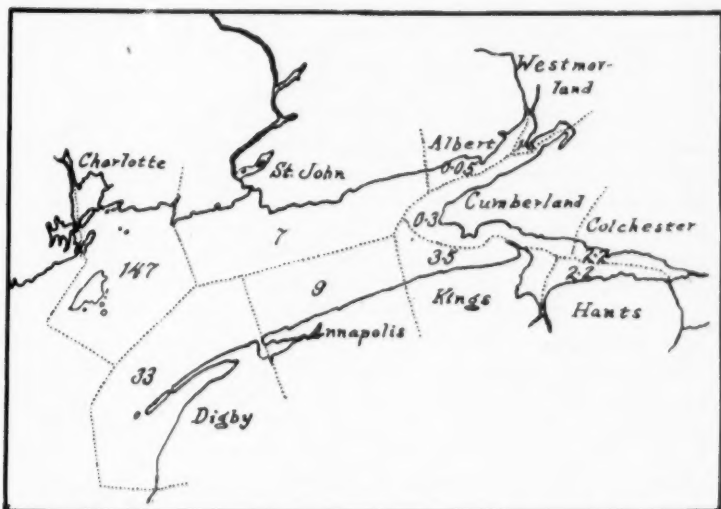


FIGURE 2.—Productivity of parts of the Bay of Fundy in pounds of fish per acre, based upon Fisheries Statistics of Canada, 1941.

The picture may be developed further where there are particularly favourable conditions. The higher production at the heads of the inlets is correlated with proximity to high discharge from rivers, and with heavy tidal mixing of this discharge with salt water. The St. John River of New Brunswick, which discharges into the Bay of Fundy about midway in its length, provides a very good test for the significance of this correlation, since it discharges a very large volume of water that comes from northern New Brunswick and Maine and from part of Quebec, and since its discharge is mixed abruptly and very thoroughly with twice as much salt water at a precise place, the Reversing Falls at the inner end of Saint John harbour. The relatively light mixture

flows out and westward along the coast at the surface, and the salt water to reach the Reversing Falls flows inward at a lower level. However this may act, it has a strikingly precise relation to fish production

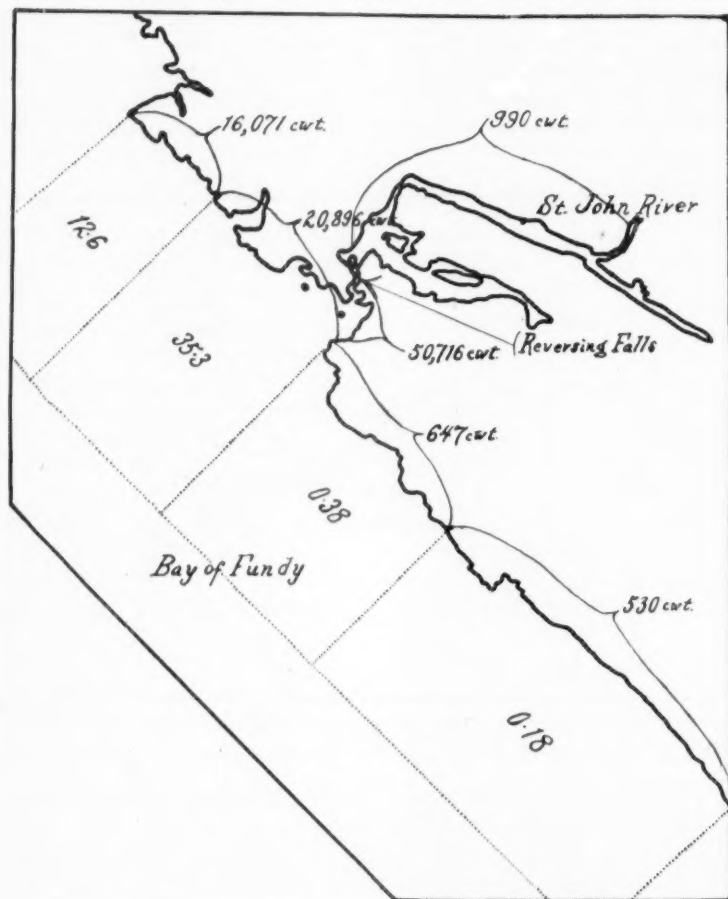


FIGURE 3.—Productivity of the waters of St. John County, New Brunswick, in pounds of fish per acre and in hundredweights of fish, based upon the fishery inspectors' reports for 1907, 41st annual report, Department of Marine and Fisheries.

as shown by the fisheries statistics. Separate figures for the landings in various parts of St. John County, which are necessary to reveal this picture, are available for the year 1907 (Fig. 3). Out of 8,886,000

pounds for the entire county, 5,071,600 pounds were for Saint John harbour, that is, for a small bit of water next to the Reversing Falls on the outside. The Kings County catch, which is for an extensive part of the slightly brackish estuary of the river inside the Reversing Falls, furnished only 99,000 pounds. For the coast outside the harbour, a fourteen-mile stretch westward along the course taken by the mixed water from the falls gave 2,089,600 pounds and a twelve-mile stretch further along this course gave 1,607,100 pounds. In most marked contrast, an eighteen-mile stretch eastward from the harbour gave only 64,700 pounds and a further stretch of thirty-three miles only 53,000 pounds. Whatever may be the explanation, the facts reveal a marked correlation between mixing of salt water with river water and high fishery yield.

In the earlier years for which fisheries statistics were collected, they were given in much greater detail. This has permitted more detailed development of the picture for the inner part of the bay. Two years were selected, 1876 and 1896, and these not only have provided the greater detail desired (Fig. 4), but they show differences from each other and from the picture for 1941 (Fig. 2). In the first place, more fish were taken in those earlier years, the poundage per acre for the whole inner part being 8.52 in 1876 and 8.6 in 1896, as compared with only 4.1 pounds per acre in 1941. Doubtless, with the fisheries of the inner part showing so little opportunity for development as compared with the outer part of the bay, the people turned to more lucrative employment. The fisheries in Charlotte County formed a decided contrast, proving to be well worth developing. They yielded 67.2 pounds per acre in 1876, 104.5 pounds in 1896, and 147 pounds in 1941. The greater details for 1876 and 1896 show that the higher yields at the heads of the inlets are related to river discharge, as is so clear for the Shubenacadie estuary, which discharges through Cobequid Bay into Minas Basin. The yields for it were 20.5 pounds per acre in 1876 and 27.5 pounds in 1896.

The greater yield for the Shubenacadie estuary in 1896 reflects a rather general situation in which there were greater differences in yields between the various districts in 1896. This is shown not only by the marked *decrease* in the yield in Cobequid Bay (from 16.2 and 3.25 pounds in 1876 to 3.4 and 0.6 pounds in 1896) as compared with the less marked *increase* in the yield in the connected Shubenacadie estuary, but also by the marked *decrease* in the yield on the north side of Minas Channel in Cumberland County (from 21.7 and 3.4 to 3 and 0.6) as compared with the less marked *increase* in the yield on the south side in Kings County (16.6 to 33.5). The facts have suggested, as pre-

sented above, that high yield is correlated with mixture of salt water with river water. Since river water is notoriously variable in amount, depending upon rainfall, it might be asked whether differences in yield are correlated with differences in river discharge.

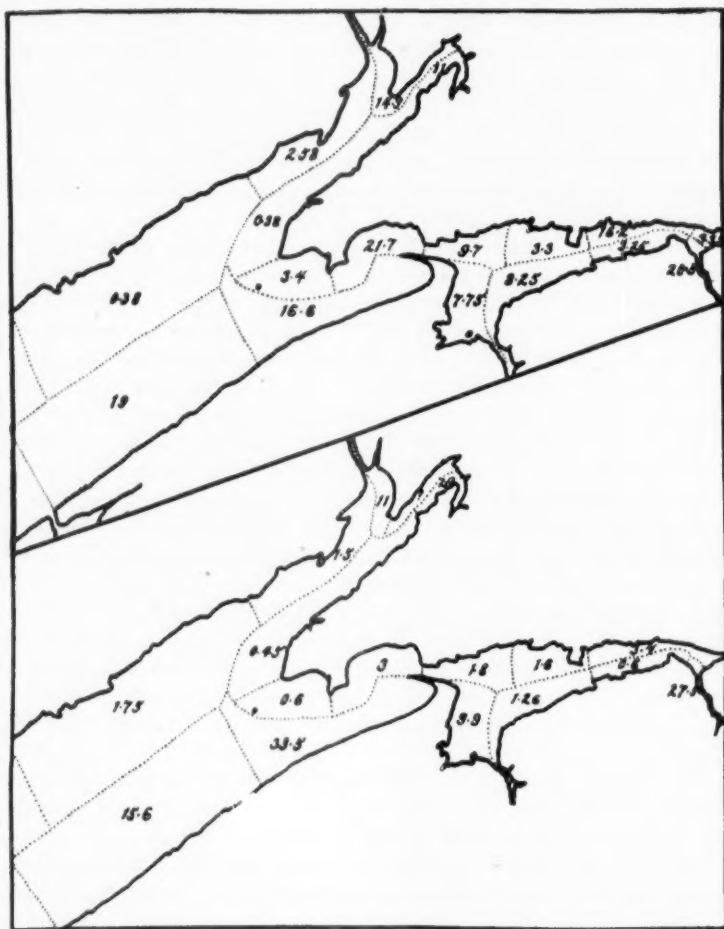


FIGURE 4.—Productivity of parts of the inner Bay of Fundy in pounds of fish per acre, based upon the fishery inspectors' reports for 1876 (top) in 9th annual report, and for 1896 (bottom) in 30th annual report of the Department of Marine and Fisheries.

While no records are available for river discharge in those years, there are records of rainfall for Truro at the head of Cobequid Bay and for Halifax near the head of the Shubenacadie River. The fisheries begin in April, are greatest in May, June, and July, and tend to end in August, as is shown by taking the monthly figures which are available for 1935. The amounts in hundredweights were reported as: March, 9; April, 130; May, 6,805; June, 7,287; July, 2,042; August, 453; September, 66; October, 0. The fisheries will be affected by the rainfall after the passing away of the spring freshets from the melting of snow and ice, which reach their peak in April. The mean rainfall in inches for Truro and Halifax for the months from May to August was: 1876, 4.74, 3.90, 2.97, 2.18; 1896, 2.00, 4.05, 7.46, 2.54. The rainfall decreased from month to month in 1876, but increased in 1896, and the total amount was one-sixth higher. With the spring freshet passing away and with plants using more and more water, decreasing rainfall has a marked effect on river flow. There is, therefore, a correlation between degree of concentration of fishery yield at places of marked mixing of river water with salt water and the amount of river water, as judged by rainfall. The Shubenacadie River water is mixed with the salt water in the estuary of the river. The water from all the rivers tributary to Minas Basin, after being mixed with salt water in the Basin and above it, is mixed with much saltier water in Minas Channel, where the salinity of the mixture rises very considerably. In these places there was greater concentration of the yield in 1896 than in 1876 in correlation with increasing rather than decreasing rainfall during the season.

THE DYNAMIC SITUATION

It has been customary, as above, to consider water productivity in terms of pounds of fish per acre and to compare it with land productivity in pounds of beef per acre, as was done by Johnstone in *Conditions of Life in the Sea* (1908). This seems to imply, as was apparently assumed in the Passamaquoddy investigations, that fish depend upon food grown locally, just as cattle feed on the local grass. But is such a static conception as applicable to movable or moving water with floating plants and animals as it is to stationary land with rooted plants? The Passamaquoddy investigations clearly refuted this conception by showing that high local production of fish is associated with low rather than high local abundance of their planktonic food and with low rather than high local production of plants that form the primary food for the animals. However, it had already been clearly shown that this conception was inapplicable to the Passamaquoddy situation, which is a

decidedly dynamic one. The herring had long been known to breed only outside the sardine region and to reach it as fry. The Bay of Fundy as a whole had been found (Huntsman, 1918) to have unusual physical conditions which render it unsuitable for successful breeding of fishes with pelagic eggs, such as cod, haddock, pollock, and hake. Such fisheries in the bay must, therefore, depend upon immigration of the fish. Also, these peculiar conditions had been seen to prevent successful reproduction of the lobster (Huntsman, 1923), and of certain floating invertebrates (Huntsman and Reid, 1921) which included the medusa *Aglantha*, the Amphipod *Parathemisto*, the Schizopod *Meganctiphanes*, and the Chaetognath *Sagitta elegans*. The last of these was carefully investigated. The Schizopod *Meganctiphanes* is an important food of the herring and is known to the fishermen as "shrimp." Investigation of the other main food of the herring, the "red feed" of the fishermen, which is largely the Copepod *Calanus finmarchicus*, had similarly shown (Wright, 1929) that this species "does not breed to any extent in the Bay of Fundy, but appears to enter that bay from the Gulf of Maine in the young state." This result for *Calanus* was confirmed (Fish, 1936a) and found to apply also to other forms of "red feed" namely *Pseudocalanus* (Fish, 1936b) and *Oithona* (Fish, 1936c).

Such evidence that the herring, which grow up in the Passamaquoddy region from the fry stage, depend for food upon animals from outside waters had made the static conception of fish production untenable, not only for Passamaquoddy Bay, but for the Bay of Fundy as a whole. Appreciation of the dynamic situation that exists is difficult for man, who from his position on land views and names the water in accordance with the basin in which it happens to be and tends to ignore the circulation which carries it and the floating plants and animals it contains from place to place over the earth. The situation is very complex, since some of the plants and the animals are attached to or remain associated with parts of the bottom, and since the locality or basin may determine to a considerable extent the character of both the water and the organisms therein. Nevertheless, the peculiarities in local fish production cannot be properly understood without taking account of the circulation that transports the organisms. Since this varies from season to season, the distribution of the organisms may be expected to exhibit great variety.

In no other part of the world is the dynamic situation for the ocean so clearly revealed as it is off our Atlantic coast. The coast extends from a degree or two south of the middle of the temperate zone northward into the Arctic zone. North of the middle, near the Grand Banks of Newfoundland, which jut out from the continent into the Atlantic,

cold waters from the arctic zone and warm waters from the torrid zone meet more than a thousand miles from where they and the life they transport properly belong. The Labrador Current carries in summer icebergs from arctic Greenland, in winter field ice with Greenland seals and other arctic mammals, and at all times varied arctic life. The so-called Gulf Stream carries Sargasso weed with its associated animals from tropic seas and at all times contains varied tropic life.

The arctic water works southwestward along our coast from Newfoundland in great eddies, and masses of the tropic water are from time to time cut off in the oceanic whirls south of Newfoundland and enter these coastal eddies. The mixed water in these eddies carries both arctic and tropic forms of life. Each form goes only as far as it is permitted to reproduce successfully or merely survive, by virtue of (1) the proportions of the contrasted constituents, (2) the rate at which the mixture flows, and (3) the strength of the local conditions including admixture of water from the land, that alter the character of the mixture. Although over five hundred miles along the course of this mixed water, the Bay of Fundy receives from time to time considerable numbers of both arctic and tropic organisms. Barrels of capelin (*Mallotus*), an arctic fish, have sometimes been taken in it, although this fish is not known to breed successfully south of Newfoundland. The arctic white whale, or beluga (*Delphinapterus leucas*), of which a colony lives in the icy cold waters of the St. Lawrence estuary at the mouth of the Saguenay River, has been seen in Passamaquoddy Bay. In 1951, an immense sluggish ocean sunfish, *Mola mola*, from the Gulf Stream was taken on the Fundy coast west of Saint John, and several of the tropic jelly-fish *Physalia*, the Portuguese man-of-war, were found at one of the entrances to Passamaquoddy Bay. Also, salps (*Salpa fusiformis*), which are tropic floating tunicates, entered that bay in swarms to die and be cast up on the beaches.

GROWTH OF PLANTS

Plants start the life cycle, since they alone have the ability to store energy from the sun for life activities, by building organic substances when in strong light. Production of life in the Bay of Fundy depends upon growth of plants there or elsewhere. Light is rather rapidly extinguished on entering water, and plants can grow only as far down in the ocean as sufficient light penetrates. This limits the attached forms to quite shallow water along shore and growth of the floating forms to a rather thin surface layer. The depth at which the amount of photosynthesis, that is, the building of organic substances, by plants just balances their respiration, that is, their use of these substances, is

known as the compensation point, and their growth is possible only at a higher level. This depth is over 100 metres in the clear and rather barren waters of the Sargasso Sea in mid-ocean and tends to be low and variable in coastal waters, being as little as 2 metres deep at times in the Firth of Clyde (Clarke, 1939). Gran and Braarud (1935) found that in the outer Bay of Fundy heavy tidal action and discharge of detritus from rivers make its waters very turbid so that sunlight does not penetrate very far. An experiment indicated that in Passamaquoddy Bay the compensation point is no deeper than 10 metres. Graham (1936) measured the transparency of the waters of the outer Bay of Fundy and neighbouring Gulf of Maine with the Secchi disc, getting values from 4.0 to 14.0 metres. The lowest were in Passamaquoddy Bay and in the St. John outflow, and the highest near Cape Sable at the mouth of the Gulf of Maine. In 1951, Mr. L. C. Dickie made readings with the Secchi disc in the outer part of Minas Basin, in Minas Channel, and thence along the Nova Scotian shore to Digby Gut. Values in the basin ranged from 1.25 off Kingsport to 4.25 metres near the north shore, in the channel from 3.00 to 3.75 metres, and along the shore of the bay from 5.75 to 10.25. As is clearly evident, the inner part of the Bay with its heavier tides and shallower water is more turbid than the outer part.

It is not merely a matter of how deep in the water there is sufficient light for plant growth. Since the floating plants (diatoms) consume as high as about one-fifth of the amount of substance they build up under the very best light, they will not grow if, through their being carried up and down by the turbulence of the water, the total light they receive is as low as one-fifth of what they would receive under continuous light of optimum intensity. In the outer part of the Bay of Fundy, the phytoplankton is poor and the poorest places are those with most turbulence, which show poor growth even in spring (Gran and Braarud, 1936). It may be safely predicted that the inner part of the bay with its more turbid water and greater turbulence is even poorer in phytoplankton.

If the Bay of Fundy is so poor for plant growth, any abundance of animals in it must enter from the Gulf of Maine. The latter shows very different conditions. There is a rich phytoplankton everywhere in April and May and this continues throughout the summer along the coast where there is turbulence. The explanation of this is that, where turbulence fails, the phytoplankton exhausts the supply of certain salts (phosphates and nitrates). Turbulence maintains the supply by bringing unexhausted, rich water from the depths and solid particles holding these salts from the bottom. Also, the light, mixed water that issues in large volume from the Bay of Fundy and moves along the coast of

Maine is rich through not having had its supply of these nutrient salts exhausted by plant growth (Gran and Braarud, 1935). The great turbulence throughout the Bay of Fundy not only largely prevents plant growth in that bay, but also provides a steady supply of rich water for plant growth to the neighbouring part of the Gulf of Maine, water that is relatively light because it contains fresh water from the rivers, chiefly the St. John, that discharge into the Bay. The bay and the gulf may be said to co-operate in producing steadily a very large amount of phytoplankton in the gulf near the mouth of the bay. The animals that take advantage of this food are somewhat in a position to be carried into the bay if at the right depth for the return current of deep salt water.

TRANSPORT OF ANIMALS

The principal animals in the Gulf of Maine to feed upon the phytoplankton are Crustacea, the Copepods, and the Schizopods. *Calanus finmarchicus* and *Meganyctiphanes norvegicus* are the outstanding representatives of these two groups and both descend to deep water in sunlight. The order in the diurnal, vertical migrations of these and other zooplanktons, including fishes, is as yet only partly elucidated. Since the currents in the Bay of Fundy and the Gulf of Maine vary considerably with depth, the depth at which these animals are swimming at any time determines where they will be carried. The complexities of their vertical movements and of the currents are so great that only major facts in the occurrence of the animals can with any confidence be attributed to specific transport, in accordance with our present knowledge of the water circulation and of the main vertical distribution of these animals.

Three types of circulation come prominently into consideration. Oscillatory movements of the water, such as the flood and ebb of the tide, bring about circulation through the action on the moving water of the rotation of the earth. This so-called Coriolis force diverts movements to the right in the northern hemisphere. Consequently, the water in a basin, such as the Bay of Fundy, circulates in a counter-clockwise fashion (Fig. 5). The mixing of light river water with heavy sea water in a channel (Fig. 6, bottom), as at the Reversing Falls of the St. John estuary, sets up hydrodynamic forces which drive the mixture oceanward at the surface and the sea water riverward at a lower level, and this has been studied for the St. John outflow (Hachey, 1935). When light water accumulates at the surface (Fig. 6, top), as in the centre of Passamaquoddy Bay from the outflow of the Digdeguash and Magaguadavic estuaries, tidal mixing along an adjacent rough

shore produces a triple circulation, both surface and deep water moving to the place of mixing and the mixture moving from the place at an intermediate level (Watson, 1936). The dependable tidal currents of the Bay of Fundy act with the discharge of river water to ensure (1) a horizontal differential in movement that gives counter-clockwise circulation around broad basins, (2) a vertical differential in movement that is related on the seaward side to channel mixing of river water with sea water and that consists of movement from the mixing place at the



FIGURE 5.—Isohalines to show salinity of water in the inner part of the Bay of Fundy and the outer part of Minas Basin, based upon Watson's (1936) data for September 8, 1932, at eight stations in the bay, and upon data obtained in 1947 at ten shore stations related to Minas Channel. All stations are indicated by crosses. Arrows represent circulation of the water as deduced from the above.

surface and movement toward it at a lower level, and (3) a triple vertical differential in movement that is related to shore mixing of stratified water and that consists of onshore movements both at the surface and at some depth and of offshore movement at an intermediate level.

Three types of animals that differ in the vertical distribution which affects their transport in the water may be distinguished. *Calanus* and *Meganctiphanes*, which on the whole keep far down from the surface, are in position for transport shoreward or riverward where such move-

ments are sufficiently deep. The Copepods *Acartia* and *Eurytemora*, which on the whole keep near the surface, are in position for transport shoreward from the middle of basins containing stratified water. The herring, which keep near the surface when small and go deeper with

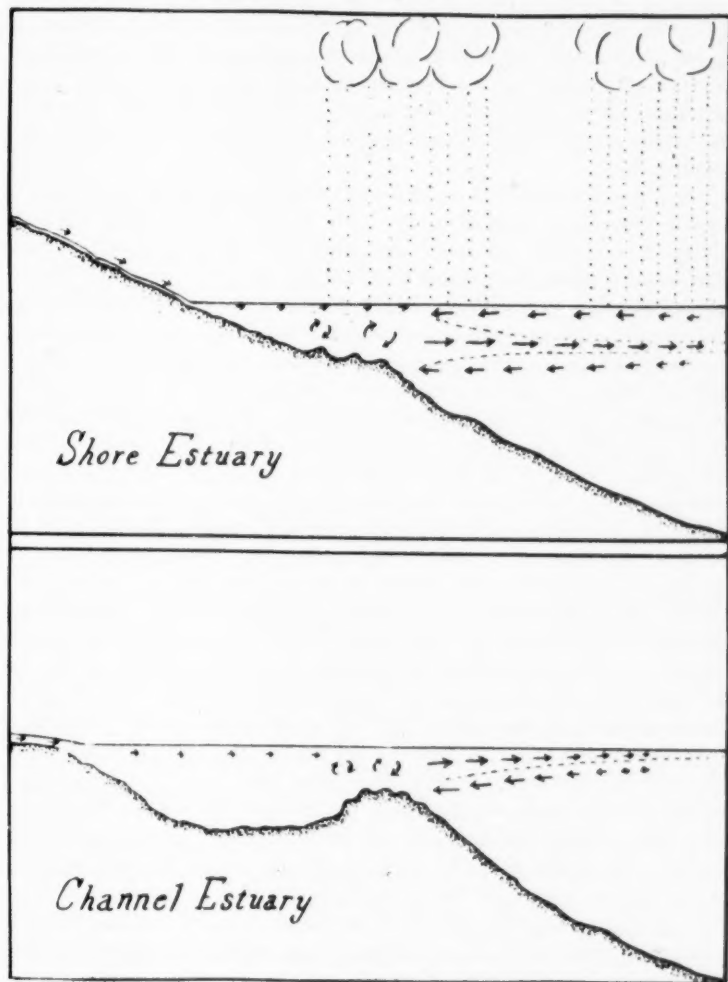


FIGURE 6.—Schematic representations of circulation engendered by shore mixing (top) and channel mixing (bottom) of light and heavy water.

increase in size, but are mainly not far from the surface except at low temperatures, are well fitted to show variations in transport with size and with season.

SOLUTION OF THE PROBLEM

At this stage in fisheries research, any solution must be considered as tentative and to be tested by much investigation. The knowledge outlined above does seem, however, to permit presentation of concrete accounts of how life is being produced in relation to the Bay of Fundy that serve to explain the great differences in productivity which the fisheries reveal.

High productivity in the outer part of the bay is clearly dependent upon indraught of food animals, if not of the fish, from the Gulf of Maine. The herring, which are responsible for the exceptionally great productivity of the Passamaquoddy sardine region, are present there throughout the year. When the adults were very numerous in the middle of the last century before the sardine industry developed, they were taken in the summer in great quantities on the outer side of Grand Manan Island, where they spawned. The spent fish could be taken during winter in such great numbers inland, even toward the head of Passamaquoddy Bay, that a big fishery for them was developed. The young enter that bay in the late larval or "eye-ball" stage, and the next stage, the britt, which is too small for canning, is concentrated there. The mechanism for this concentration is seen to be that, as a result of their habit of keeping to the surface, they are carried from the stratified water of the outer Bay of Fundy to the mixing places just outside and in the entrances to Passamaquoddy Bay. The Coriolis force ensures slow circulation of water into that bay through Letite Passage which is on the right going inward. Inside the bay, extensive mixing of the stratified water near the shore, from the middle of the west, or inner, side to the head takes such surface forms thitherward and thus holds and concentrates them in the bay. As the herring get larger, they go deeper in the water and tend to be carried from the mixing places to the centre of the bay and thence, in the outward movement, from the bay, which from the action of the Coriolis force is through Head Harbour Passage on the right going out. The larger the herring get, the farther out are they distributed on the whole (Fig. 7), until as adults they are almost entirely outside Grand Manan during the summer.

The very great quantities of these herring, which are brought to the region as larvae and which are largely held in it throughout their lives, must have food. Their growth shows that food is brought to them in ample quantity. That it is brought to them in more than ample quanti-

ty in some places and at some times is shown by the extraordinary fatness of those taken from Head Harbour Passage, or Quoddy River. Before canning of the young began, "Quoddy River herring" of unexampled fatness were fished in that passage, these being at the stage before spawning when herring are fattest. On occasion, the deep-water Schizopods or "shrimp" that must have come from the Gulf of Maine are cast up on the Campobello shore of the passage in such great



FIGURE 7.—Schematic representations of differences from place to place from Saint John to Passamaquoddy Bay and Grand Manan Island in the prevalent sizes of the herring taken, as reported in 1933 by four different men who transport fish to the factories of the region.

quantities as to be carted away for manure. Also, I have been in a weir on that shore when it contained herring that after many days confinement were still unsaleable from being full of "red feed," and I found *Calanus* so abundant as to make the water feel gritty. The mechanism that makes this food available to the herring that are near the surface consists first of the deep return current that brings these deep-water forms from the Gulf of Maine to the deep water just outside the passage. Next is the working out through the passage of the mixed water from

discharge of a heavy freshet into Passamaquoddy Bay. As found in 1933 and again in 1951, the strong reflux that this engenders brings the deep-water forms into the Passage in large quantity. There, they are brought to the surface in the tidal boils and carried by the tidal flow into the adjacent shallow inlets of Harbour de Loutre and Cobscook Bay, where they are rather steadily available to the fish. Their tendency to keep deep down in the water unless carried upward ensures that they are not removed from the passage in the superficial outflow, but remain to serve as food for fishes and also, at the very surface, for birds.

The small herring or britt that are concentrated in Passamaquoddy Bay grow too rapidly to become very fat. Their food is not provided through Head Harbour Passage, which is fully occupied by the outflow from the bay. The Coriolis force determines inflow through Letite Passage, which, although shallow, is so short that quite salt water enters during the latter part of the flood tide. This water is a mixture of surface and deep water from outside and thus contains both surface forms, such as *Acartia*, and deep forms, such as *Calanus*. Inside the passage, the water is rather deep and little turbulent. The deep forms descend and fail to be carried back out with the ebb tide and accumulate in the bottom water of the bay. The surface forms are carried back out to some extent, but, on the whole, work inward. Like the small herring, they are held in the bay because they are carried to the mixing places on the west shore and at the head. The deep forms are also carried to the mixing places, where both kinds become concentrated with the britt, thus permitting the latter to feed upon them. In 1951 this concentration of the britt and of the surface and deep Copepods was so favourable for the feeding of the britt that in August the surface of the bay was thickly peppered with their excreta and when they were large enough in the fall for canning, more than ten million pounds were taken by the weirs near the mixing places.

The small herring are not only concentrated with suitable food animals, but they are segregated from the larger herring which would compete with them for food. In addition, they are kept from their enemies. The mackerel (Fig. 8), for example, and also the dogfish are carried into the bay along the Nova Scotian coast, where they occur in fairly large numbers, but few of them reach the Passamaquoddy region.

Head Harbour Passage and the inner part of Passamaquoddy Bay provide the most striking illustrations of the process by which the large quantities of herring are produced that are taken in the Passamaquoddy region from Saint John to the mouth of the Bay of Fundy. The very heavy discharge from the St. John River, which is mixed with an

immense amount of sea water as it passes out through this region, causes the circulation that brings the animals in from the Gulf of Maine. Through this circulation, the region is able to draw upon the Gulf of Maine as well as upon the Bay of Fundy for its supplies of larval herring and of herring food.

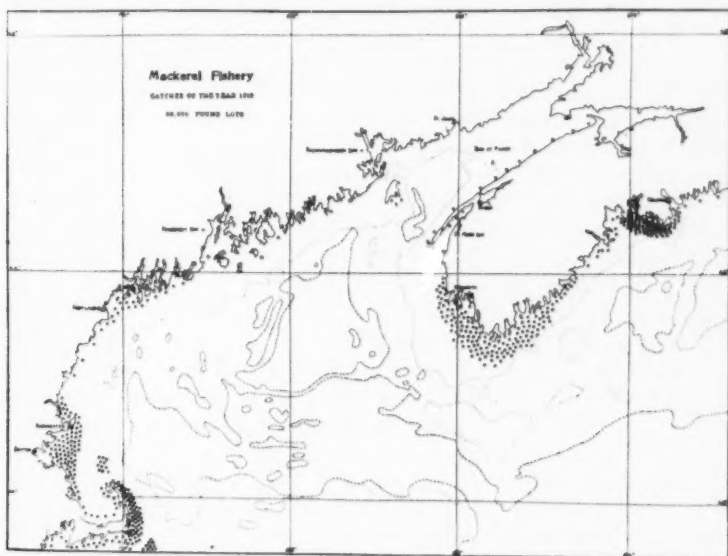


FIGURE 8.—Catches of mackerel from Cape Cod to Halifax in 1919, each dot representing 50,000 pounds. Bay of Fundy at top on right. Prepared by Dr. A. W. H. Needler.

The concentration of fish near and inside Saint John harbour as far as the Reversing Falls is a different, but cognate phenomenon. While food animals for the fish are brought riverward in the return current, even as far as the harbour, this current is in part so near the surface where the outflow from the harbour spreads out over the bay (Fig. 9) that near-surface fishes such as the wandering adult salmon are carried riverward and concentrated in and near the harbour, where their capture is then particularly easy and profitable.

The inner part of the Bay of Fundy has such turbulent water that the deep forms such as *Calanus* that enter the outer part from the Gulf of Maine are carried but slowly into it. They are almost as often near the surface in the outward moving water as near the bottom in the inward moving water. Owing to the Coriolis force, there is a general inward

movement along the Nova Scotian shore so that planktonic surveys show more fish food from the Gulf of Maine along this shore than along the other, just as the fishery results show more fish. The inward movement ends rather abruptly at the mouth of Minas Channel, where there is no longer scope for the Coriolis force to operate. The very great turbulence in this Channel, by moving the animals up and down, prevents forms



FIGURE 9.—Schematic representation of sub-surface circulation in the St. John outflow from Saint John to Grand Manan Island, as deduced from salinities.

that ordinarily are deep in the water from being carried inward by the inflow near the bottom, and forms that ordinarily are near the surface from being carried outward by the outflow near the surface. Floating material, such as branches of trees and fishing buoys, that may be brought to the mouth of the channel in the inward movement along the Nova Scotian shore of the bay are prevented by the surface outflow from penetrating the channel, and accumulate at the mouth in a dense mass that is known locally as the "cedar swamp." Drift bottles similarly reach the mouth of the channel and rarely penetrate it for any

distance. Fish that keep deep in the water in spite of the turbulence are carried in, so that some cod, haddock, hake, and halibut are taken inside Minas Basin. Lighter water on the New Brunswick side of the inner bay produces surface movement across the bay from New Brunswick to Nova Scotia. This enhances the difference between the two sides of the bay, making the New Brunswick fishery much poorer than that of Nova Scotia.

As judged from the plankton, Minas Channel is the most barren part of these waters in fish food (E. Jermolajew, unpublished). Crustacea from the Gulf of Maine just fail to reach it and, although not yet investigated, local growth of plants would seem to be at a minimum in spite of the richness of the water in nutrient salts. That phytoplankton in the inner Bay of Fundy is inadequate to provide food for the growth of microcrustacea which serve as food for fish is shown by the condition of the few *Calanus* that are carried far into the bay. They have been found to be nearly devoid of the oil that is so conspicuous as a very large globule in a well-fed individual. Those that enter the Passamaquoddy region from the gulf have more oil in them than the herring can digest, as is indicated by the fact that the masses of herring that have fed on *Calanus* can be readily located by the oil "slick" made by their excreta on the surface of the water.

That the amount of fish increases from Minas Basin to Cobequid Bay and to the Shubenacadie estuary requires explanation. If low production of phytoplankton in the inner bay and in Minas Channel is due to the turbulence preventing the floating plants from remaining long enough sufficiently near the surface to receive the amount of light required for their growth, the amount of growth should increase as the depth decreases, since the shallower the water the less far will they be taken from the surface by the turbulence. This matter has still to be investigated, but study of the zooplankton (E. Jermolajew, unpublished) has shown that the amount of microcrustacea available to fish for food increases from Minas Channel to the Shubenacadie estuary and it consists of estuarial species such as *Acartia tonsa* and *Pseudodiaptomus coronatus* that cannot have come from outer waters. Tows made in 1951 showed the following numbers of zooplanktons: Minas Channel with water as deep as 57 fathoms, 4,700 and 5,700; Minas Basin (southern bight) with water as deep as 13 fathoms, 14,800 and 25,400; Cobequid Bay with water as deep as 10 fathoms, 50,200 and 89,900; Shubenacadie estuary with water as deep as 3 fathoms, 253,800.

However, a very shallow estuary with heavy tides and turbulent water is not necessarily more productive than a deep one. The inner, shallow part of the Petitcodiac estuary of the northern branch of the

Bay of Fundy yields practically no fish. The deeper outer part has a fishery for salmon and shad, which are concentrated toward its head where the salter water flowing in below begins to be thoroughly mixed with the outflow of less salt water. The shallow inner part, which is twenty miles long, is traversed by a tidal bore. The breaking tidal wave churns up the estuarial water with the silt of the bottom to make a heavy suspension of clay, which buoys the animals up to the surface where they become prey for birds. What plants are produced in it has not been investigated, but it presents a distinct hazard for animals, and those that enter it, such as salmon, pass through it very slowly owing to the great turbulence.

SUMMARY

Striking differences in the amounts of fish taken in different parts of the Bay of Fundy reflect differences in local abundance of fish. These differences receive explanation from knowledge of where the plants and animals which make up the food chain are grown and of how they are transported by the circulation of the water.

Great rise and fall of the tide in the bay makes the water turbulent and hence, as a whole, both turbid and rich in nutrient salts for plant growth from updraft of bottom water and sediment. The turbidity and the turbulence largely prevent growth of floating plants, which fail to remain long in the thin surface layer which alone has sufficient light. The turbulence mixes river water, which comes in largest amount from the St. John River through Saint John harbour, with many times its volume of sea water, and the relatively light mixture, which is rich in nutrient salts, flows out into the Gulf of Maine. Where it spreads near the surface it yields a heavy and continuous growth of phytoplankton in accordance with temperature and light. The animals, mainly microcrustacea, which feed upon the phytoplankton are carried into the bay in the deep return current and in the general counter-clockwise circulation of gulf and bay, in accordance with the depths at which they live.

The heavy discharge of the St. John River and of the rivers tributary to Passamaquoddy Bay, when mixed with much sea water, ensures, through return currents, more or less steady and large supplies of the microcrustacea for the food of fishes in the outer part of the Bay of Fundy. The Passamaquoddy mechanism, a complex circulation of the water, concentrates the herring from the late fry stage onward, and the microcrustacea for their food, in that region. It also segregates the sizes of herring, makes the microcrustacea available near the surface where the herring live, and largely concentrates the small herring and the

zooplankton suitable for their food far inland, where they are relatively free from enemies and from competition for food.

The zooplankton from the Gulf of Maine is carried into the inner part of the Bay of Fundy but slowly, owing to the very great turbulence, and enters mainly along the Nova Scotian shore. Such food for fish decreases in amount going inward and becomes poor through lack of phytoplankton for food. It fails to enter Minas Channel, which is most barren of plankton.

With decreasing depth from Minas Channel to the Shubenacadie estuary, conditions for growth of phytoplankton improve, since turbulence cannot take these organisms far from the light near the surface. In accordance with this, the planktonic microcrustacea, consisting of locally produced estuarial forms, increase in amount and so do the fish. Although very shallow, the inner part of the Petitcodiac estuary is very barren because it is traversed by a tidal bore, which through suspended silt buoys animals to the surface to become prey for birds.

The local abundance of fish which determines large catches is to a considerable extent attributable merely to the transport and concentration of the fish by the circulation of water.

REFERENCES

- CLARKE, G. L. (1939). The utilization of solar energy by aquatic organisms. Publ. Amer. Ass. Adv. Sc., **10**: 27.
- FISH, C. J. (1936a). The biology of *Calanus finmarchicus* in the Gulf of Maine and Bay of Fundy. Biol. Bull., **70**: 118.
- (1936b). The biology of *Pseudocalanus minutus* in the Gulf of Maine and Bay of Fundy. Biol. Bull., **70**: 193.
- (1936c). The biology of *Oithona similis* in the Gulf of Maine and Bay of Fundy. Biol. Bull., **71**: 168.
- FISH, C. J. and JOHNSON, M. W. (1937). The biology of the zooplankton population in the Bay of Fundy and Gulf of Maine with special reference to production and distribution. J. Biol. Bd. Can., **3**: 189.
- GRAHAM, M. (1936). Investigations of the herring of Passamaquoddy and adjacent regions. J. Biol. Bd. Can., **2**: 95.
- GRAN, H. H. and BRAARUD, T. (1935). A quantitative study of the phytoplankton in the Bay of Fundy and the Gulf of Maine including observations on hydrography, chemistry and turbidity. J. Biol. Bd. Can., **1**: 279.
- HACHEY, H. B. (1935). Tidal mixing in an estuary. J. Biol. Bd. Can., **1**: 171.
- HUNTSMAN, A. G. (1918). The effect of the tide on the distribution of the fishes of the Canadian Atlantic coast. Trans. Roy. Soc. Can., 3rd ser., **12**(sec. IV): 61-7.
- (1923). Natural lobster breeding. Bull. Biol. Bd. Can., **5**: 1.
- (1928). The Passamaquoddy bay power project and its effect on the fisheries. Saint John, N.B. Pp. 1-45.
- (1934). Herring and water movements. In James Johnstone Memorial Volume, pp. 81-96. Liverpool.

- (1938). International Passamaquoddy fishery investigations. *J. Cons. Inter. Explor. Mer.*, **13**: 357.
- HUNTSMAN, A. G. and REID, M. E. (1921). The success of reproduction in *Sagitta elegans* in the Bay of Fundy and the Gulf of St. Lawrence. *Trans. Roy. Can. Inst.*, **13**(2): 99.
- JOHNSTONE, J. (1908). *Conditions of life in the sea*. Cambridge: Cambridge University Press. Pp. 1-332.
- UNITED NATIONS, FOOD AND AGRICULTURAL ORGANIZATION (1950). *Yearbook of fisheries statistics, 1948-49*. Pp. 1-312.
- WATSON, E. E. (1936). Mixing and residual currents in tidal waters as illustrated in the Bay of Fundy. *J. Biol. Bd. Can.*, **2**: 141.
- WRIGHT, N. (1929). In J. J. Cowie: Report on the work of the Biological Board for 1928-29. *Ann. Rep. Fisher. Br., Dep. Mar. Fisher. Can.*, **62**: 123.

Thyroid Function in Some Anadromous and Landlocked Teleosts

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Presented by W. A. CLEMENS, F.R.S.C.

INTRODUCTION

ANADROMOUS teleost fishes of many species, although usually migrating to sea as juveniles, may complete their entire life cycle in fresh water. This frequently occurs in lake regions, remote from the sea, where the fish are referred to as "landlocked." The members of some anadromous species migrate soon after hatching; others have a prolonged juvenile, stenohaline freshwater phase. The smelt (*Osmerus mordax*), alewife (*Pomolobus pseudoharengus*), chum (*Oncorhynchus keta*), and pink salmon (*O. gorbuscha*) are representatives of the first group, while the sockeye (*O. nerka*), coho (*O. kisutch*), and Atlantic salmon (*Salmo salar*) belong to the second. This latter group shows a distinct physiological transformation prior to seaward migration (Hoar, 1951).

The success of the different species when landlocked is evidently quite variable (Table I). At one extreme is the smelt which grows as

TABLE I
LENGTHS OF ANADROMOUS FISH MATURING IN MARINE OR FRESHWATER HABITATS
(Measurements given are for the older age groups but are not necessarily the maximum lengths.)

Species	Length (mm.)		Authority
	Marine	Freshwater	
<i>Salmo salar</i>	480*	350	Wilder (1947)
<i>Oncorhynchus nerka</i>	820	200-400	Carl and Clemens (1948)
<i>Pomolobus pseudoharengus</i>	258	145	Pritchard (1929)
<i>Osmerus mordax</i>	150-250	150-250	McKenzie (1946); Vladykov and McKenzie (1935) Dymond (1944); Van Oosten (1944)

*Grilse or salmon maturing after 1 year in the sea. Older fish may reach 1200 mm. (Carl and Clemens, 1948).

well in lakes as in the ocean. At the other extreme, the alewife matures at a much smaller size in lakes and shows a spectacular annual mortality (Pritchard, 1929). In general, landlocked teleosts seem to grow more slowly than the marine forms but are not subject to the annual mortality shown by the alewife.

Several writers have emphasized the importance of thyroid hormone in growth regulation of fishes. In addition, there is an evident relationship between osmotic regulation and thyroid activity. The literature has recently been reviewed (Hoar, 1951) and need not be discussed in detail here. It is sufficient to note that marine fish placed in dilute sea water show increased thyroid activity (Leloup, 1948; Olivereau, 1948) and that some anadromous fish retained in fresh water beyond the natural time of seaward migration develop hyperplastic thyroids (Hoar and Bell, 1950). The latter observation is not unexpected if the first is true, since the seaward migrating fish must have many of the physiological characteristics of a marine fish. The biochemical changes which occur in Atlantic salmon prior to seaward migration have now been studied in some detail. The elevation in blood iodine (Fontaine and Leloup, 1950a), in blood copper (Fontaine, 1948), and in degree of unsaturation of body fats (Lovern, 1934) all combine to change the tissues of the freshwater salmon parr toward the marine salmon at the time of smolt transformation. These investigations suggest, then, that thyroid hormone enters into the metabolic chains involved in the elimination of water and that the anadromous teleost making a prolonged stay in fresh water is under added osmotic stress which demands additional thyroid hormone. Such a suggestion agrees with current views on the metabolic role of thyroid hormone in other vertebrates since the elimination of water against an osmotic gradient requires a considerable expenditure of energy.

Changes in thyroid activity of alewives and smelt from coastal and landlocked environments are described in this paper as further evidence of the functions of the thyroid hormone in anadromous teleosts. Conclusions are based on histological evidence. It is recognized that the variations in thyroid function are reflected in well-marked changes in the microscopical picture of the gland (Ham, 1950). The follicles of a quiescent thyroid contain an abundance of stored colloid which is homogeneous and brightly acidophilic. The follicular colloid in the stimulated gland becomes progressively more granular and basophilic owing to enzymatic hydrolysis (de Robertis, 1949). It may eventually disappear entirely. The vacuoles frequently observed at the periphery of the follicles, although artefacts in themselves (de Robertis, 1949), are further evidence of stimulation. The epithelial

cells of the stimulated thyroid increase in number and height. Increased vascularity is also characteristic and colloid material is often observed in the vascular channels.

MATERIALS AND METHODS

The fish whose thyroids are described in this paper came from a number of different places (Table II). A. G. Huntsman collected juvenile alewives (*Pomolobus pseudoharengus*) from the Grand Lake region of Nova Scotia. Adult alewives were obtained from the Kennebecasis estuary, New Brunswick, through the co-operation of L. R. Day and J. C. Medcof. R. A. McKenzie provided juvenile and mature smelt (*Osmerus mordax*) from the Miramichi River and estuary in New Brunswick. The landlocked alewives and smelt from the Great Lakes were contributed by F. E. J. Fry and J. J. Graham. The co-operation of all those who have made the study possible is gratefully acknowledged.

Bouin's picric-acid-formol-acetic-acid mixture was the fixative of choice. However, some of the fish used were taken from routine formalin collections made for other purposes. This is particularly true of the fish from Ontario. Thyroids were embedded in paraffin, sectioned serially at 7μ or 10μ and stained with Harris' hematoxylin and eosin. Merva K. Cottle made most of the preparations but Dorothy Hamilton also spent many hours on the project. It is a pleasure to thank them for the care and skill with which they put so many thyroids on glass. Financial assistance for this part of the project was obtained from a University Research Grant.

RESULTS

Alewives

Juvenile seaward migrants from the Atlantic coast. Thyroids of migrants (25 to 65 mm. total length), collected during the latter part of July, are uniformly quiescent. In the smaller fish the gland is incompletely developed. Small, spherical, differentiating follicles are scattered widely. The epithelium is squamous or low cuboidal; the colloid brightly eosinophilic, highly refractile and abundant (Fig. 1). Fish 50 to 60 mm. in length have well-differentiated thyroids with the glandular tissue characteristically distributed about the ventral aorta. The follicles are larger, made up of cuboidal cells, and contain abundant, eosinophilic colloid (Fig. 2). The texture varies from highly refractile to slightly granular. Colloid is sometimes conspicuous in the lymphatics.

Specimens collected from the Lower Rawdon River a month later

TABLE II
THYROIDS EXAMINED HISTOLOGICALLY

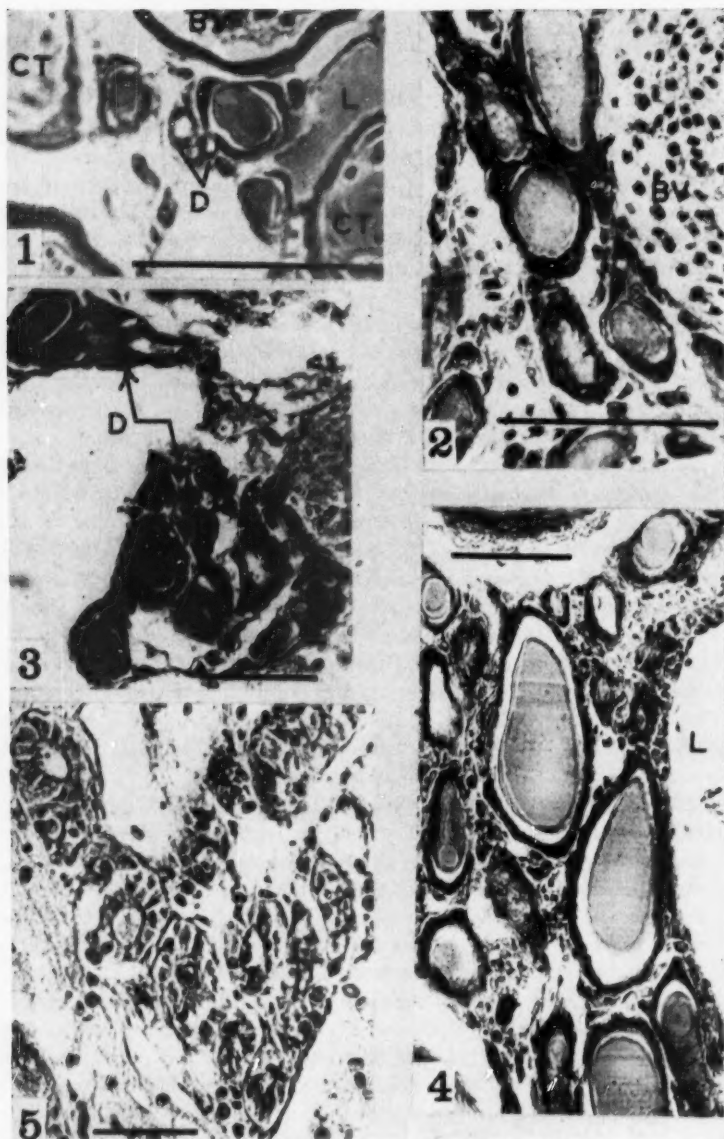
<i>Place of capture</i>	<i>Date</i>	<i>Maturity</i>	<i>Length of fish (mm.)</i>	<i>Number</i>
ALEWIVES				
Fletcher Dam, N.S.	July 24-6, 1949	seaward migrants	25-65	15
Lower Rawdon River, N.S.	Aug. 22, 1949	"	95-100	4
Milledgeville, N.B.	Feb. 1951	maturing adults, estuary	300-350	4
Hamilton Beach, Ont.	May 1950	adults, prespawning	135-190	8
Bay of Quinte, Ont.	Aug. 1950	post-spawning adult	150	1
" " "	May 1950	mortality victim	172	1
Gananoque River, Ont.	June 1950	adult	155-165	2
SMELT				
Miramichi, N.B.	July-Sept. 1942	seaward migrants	30-50	10
South Bay, Ont.	July 1951	juveniles of the year	25-30	3
Miramichi estuary	May 7, 1951	immature yearlings	100-105	3
South Bay, Ont.	April 1950	spawning run	140-165	7
" " "	April 28, 1951	"	140-165	5
Miramichi River	May 9, 1949	spawning and spent	140-198	7
Miramichi estuary	Sept. 8, 1949	adults	170-185	2

are about twice as large (95 to 100 μ m.). The thyroids are more active than those of the younger fish but do not show the marked activity characteristic of seaward migrating salmon smolt of comparable size (Hoar, 1939). Proliferation of new thyroid follicles, however, is apparent (Fig. 3) and the thyroid mass is evidently extending. The epithelium is cuboidal, at times approaching a columnar type. In places the colloid is almost completely withdrawn but more often it is abundant, homogeneous, and eosinophilic (Fig. 4). The follicles are larger at this stage (25 to 50 μ m in contrast to 15 to 30 μ m in the 50 mm. fish) but this increase is not out of proportion to the increased size of the fish. The thyroids are similar to those of migrating Pacific salmon found in coastal areas (Hoar and Bell, 1950). There is no marked increase in activity associated with the seaward migration.

Sexually mature adults from the Atlantic coast. Thyroids from fish in this group are characterized by the mild state of activity which is apparently normal for sexually maturing teleosts (Fontaine *et al.*, 1948; Fontaine et Leloup, 1950b). The epithelium varies from cuboidal (Fig. 6) to low columnar (Fig. 5). Many follicles contain refractile, eosinophilic colloid riddled with peripheral vacuoles. These vacuoles are not always present, however, and the colloid may be more basophilic. In many areas the colloid is absent, and the smaller follicles of columnar epithelium contain only a fine reticulum (Fig. 5). The two types of follicles are present in different parts of the same gland and frequently occur in the same histological section. The gland is active but in no case hyperplastic or exhausted.

Mature alewives from Lake Ontario. These thyroids differ markedly from those of the Atlantic coast fish just described. The glands are extremely hyperplastic and in many cases appear to be exhausted. Empty follicles are packed in masses about the blood vessels and lymphatics. They extend into the connective tissue spaces around the muscle masses and into the cavities of the basibranchial bones (Fig. 7). Colloid-containing follicles were located in only five of twelve thyroids examined in serial sections. One thyroid was pathological. In this gland organized follicles were absent and the thyroid area was infiltrated with masses of lymphocytes (Fig. 9). No particular significance can be attached to this since a pathological gland was also found in one of the larger juveniles from the Lower Rawdon River (Fig. 10). Similar pathologies have been previously described in thyroids from fish (Gaylord and Marsh, 1912).

Large masses of empty follicles are the most characteristic feature of the thyroids from the landlocked alewives. The epithelium is uniformly cuboidal or low columnar and never assumes the high



Legend for all plates: B, bone; BV, blood vessel; C, colloid; CT, cartilage; D, differentiating follicles; L, lymphatic; V, peripheral vacuoles.

PLATE I.—Photomicrographs of sections of thyroid glands of alewives from the Atlantic coast, locations given in Table II. Horizontal line on each figure is 50μ . FIGURE 1.—25 mm. fry. Small differentiating follicles near well-formed colloid-containing follicles. FIGURE 2.—55 mm. fry. FIGURE 3.—100 mm. juvenile. FIGURE 4.—98 mm. juvenile. FIGURE 5.—Maturing adult from estuary. Follicles contain only fine basophilic reticulum.

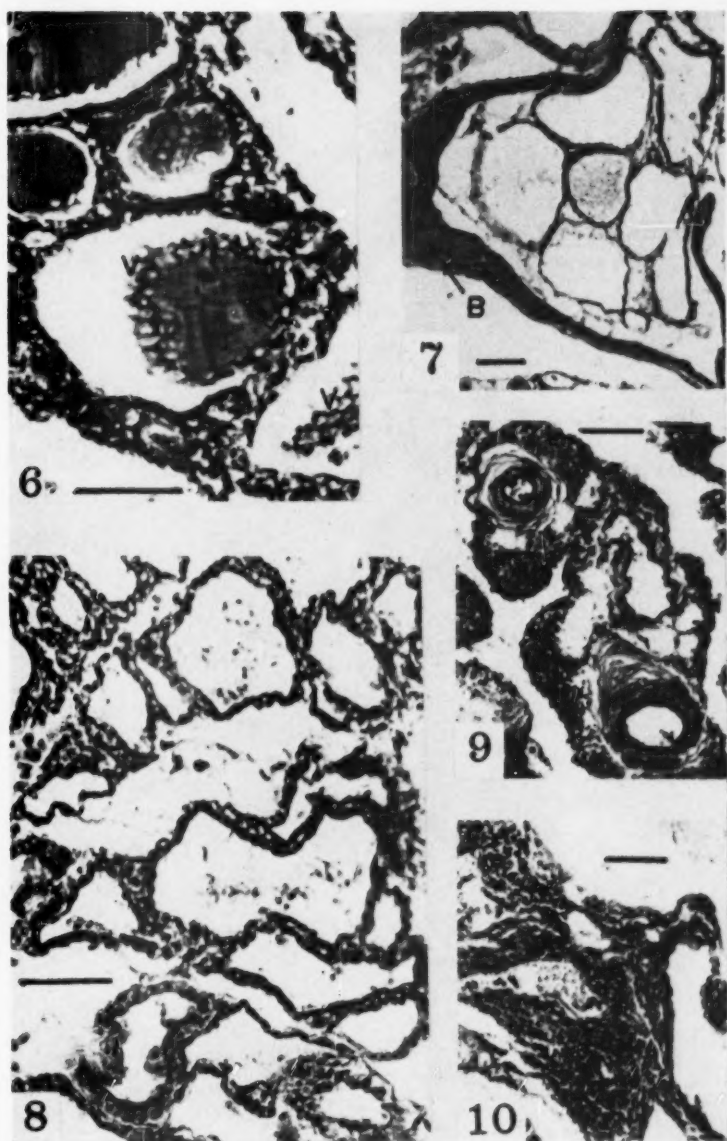


PLATE II.—Photomicrographs of sections of thyroid glands from alewives. Horizontal line on each figure is 50μ . FIGURE 6.—Maturing adult from Kennebecasis estuary. Follicular epithelium is low and colloid shows peripheral vacuoles. FIGURE 7.—Mature adult, Hamilton Beach, Ont. Seven empty follicles almost surrounded by basibranchial bone. FIGURE 8.—Same as Fig. 7 showing numerous empty follicles. FIGURE 9.—Mature fish, Bay of Quinte, Ont. Mass of tissue from pathological thyroid runs diagonally across field. FIGURE 10.—95 mm. juvenile from Lower Rawdon River, N.S. Masses of unorganized cells in pathological gland.

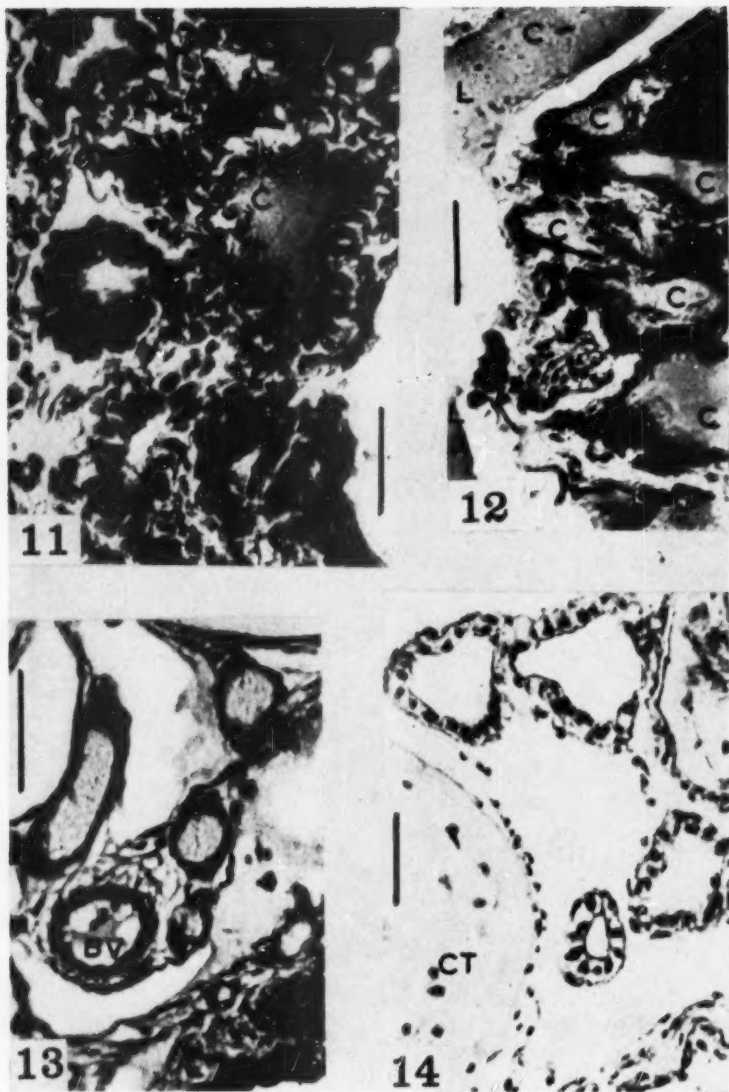


PLATE III.—Photomicrographs of sections of thyroid glands. Vertical line on each figure is 25μ . FIGURE 11.—Mature alewife from Gananoque River, June 1950. Follicles with high cuboidal or columnar epithelium sometimes contain eosinophilic colloid. FIGURE 12.—Same as Fig. 11. Colloid in follicles and lymphatics is eosinophilic. FIGURE 13.—30 mm. smelt from Miramichi River. Granular basophilic colloid in follicles. FIGURE 14.—30 mm. smelt from South Bay, Ont. Four empty follicles.

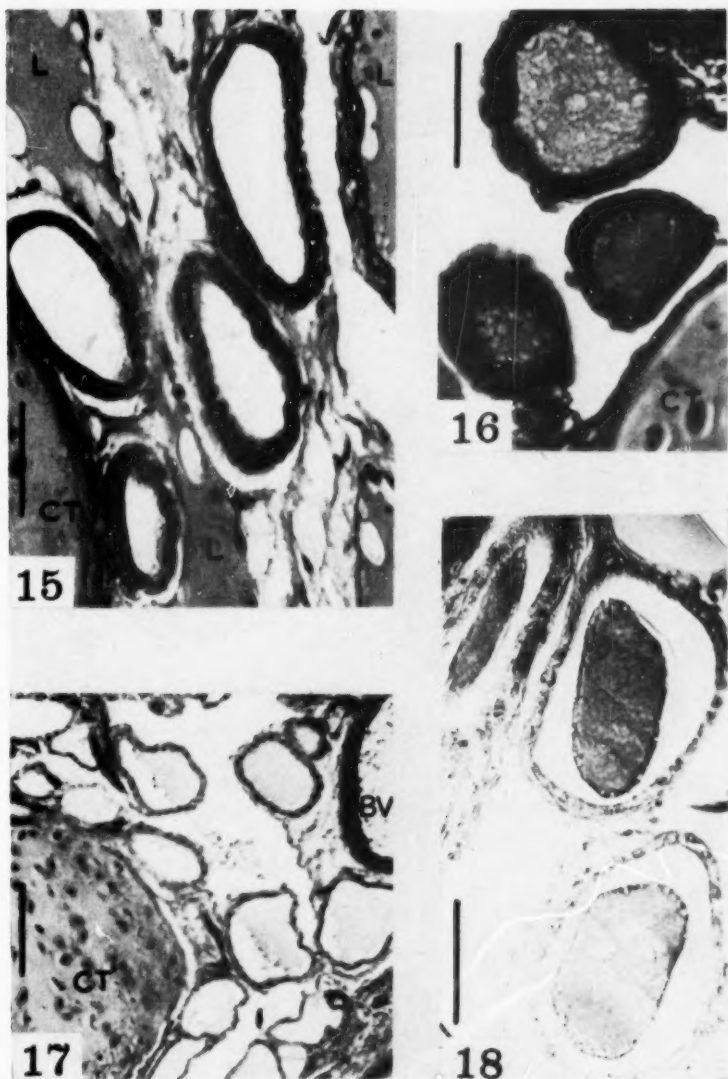


PLATE IV.—Photomicrographs of sections of smelt thyroid glands from Miramichi River and estuary. FIGURE 15.—50 mm. fry. Empty follicles, colloid in lymphatics. Vertical indicator line is 25μ . FIGURE 16.—50 mm. fry. Basophilic granular colloid. Vertical indicator line is 25μ . FIGURE 17.—Immature yearling smelt (105 mm.) from tide water. Vertical indicator line is 100μ . FIGURE 18.—170 mm. adult male from estuary in September. Cuboidal epithelium, acidophilic colloid with some peripheral vacuoles. Vertical indicator line is 50μ .

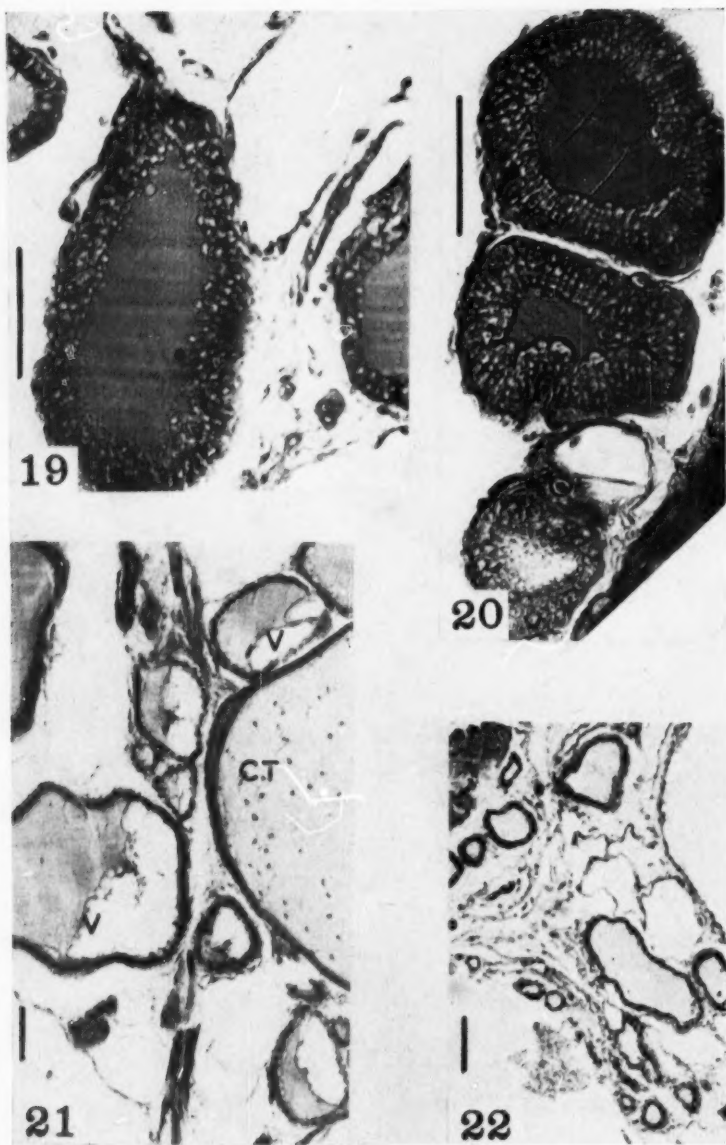


PLATE V.—Photomicrographs of sections of thyroid glands from smelt. Vertical line on each figure is 50μ . FIGURE 19.—175 mm. female, spent and leaving spawning grounds May 1949, Miramichi River, N.B. FIGURE 20.—165 mm. male about spent and leaving spawning grounds May 1949, Miramichi River, N.B. FIGURES 21 and 22.—Mature smelt from spawning run, South Bay, Ont., April 28, 1951.

columnar form often characteristic of very active thyroids. Follicles are large and irregular in shape indicating an overgrowth of the epithelial cells. The absence of stainable colloid is a striking feature. These characteristics are illustrated in Fig. 8.

As previously mentioned, colloid-containing follicles were present in about 50 per cent of the glands studied. One thyroid examined, from an adult in the post-spawning condition, contained many such follicles but the other four showed only a relatively insignificant number. These colloid-containing follicles are usually small (25 to 35 μ in diameter), lined with high cuboidal or columnar epithelium, and contain brightly acidophilic colloid (Fig. 11). They are sometimes isolated but more often in small groups. The presence of colloid in the lymphatics is a characteristic feature (Fig. 12).

Smelt

Juvenile underyearling smelt. Smelt fry of 25 to 30 mm. total length were available from coastal areas and from the Great Lakes. In both cases the thyroid gland is differentiating and has not yet attained its final distribution. These developing thyroids all show evidence of activity. This activity, however, is more marked in the landlocked fish. Thyroids from the coastal smelt fry are characterized by cuboidal epithelium, some basophilic follicular colloid, and an abundance of colloid in the lymphatics; thyroids from the Great Lakes smelt fry show high cuboidal epithelium and an absence of follicular colloid. Figs. 13 and 14 show the contrast.

Larger juveniles (40-50 mm.) are available only from the Miramichi. The thyroid glands are larger. Although stored colloid is usually more abundant it may be entirely absent (Fig. 15). When present, it stains slightly basophilic (Fig. 16). Colloid is conspicuous in the lymphatics and blood vessels (Fig. 15). These mildly active thyroids do not differ greatly from those of the smaller fry.

Immature yearling smelt from the estuary. Thyroids of these fish are similar to those of the seaward migrating fry. The relatively large follicles are made up of a cuboidal epithelium and are either empty or contain a somewhat basophilic colloid with prominent peripheral vacuoles (Fig. 17). The epithelium is often folded. Colloid is conspicuous in the blood vessels and lymphatics.

Spawning smelt from the Miramichi River. The thyroid follicles of the spawning smelt are bounded by columnar or high cuboidal epithelium and filled with brightly acidophilic, highly refractile colloid (Figs. 19 and 20). Peripheral vacuoles are rarely seen and colloid is not evident in the vascular channels. Colloid storage, therefore, seems characteristic of spawning Atlantic smelt as well as salmon (Hoar, 1939; Fontaine *et al.*, 1948).

It is interesting that the follicular epithelium of male fish at spawning time is high columnar (Fig. 20), that of the females low columnar or high cuboidal (Fig. 19). This contrast between the thyroids of the two sexes was consistent in the three males and four females examined. Empty follicles were occasionally found in the thyroids of female smelt and the lower epithelium, contrary to the usual situation (Ham, 1950), seems to indicate a more active gland in these fish.

Post-spawning smelt from the Miramichi estuary. These fish were collected in September and had probably spawned during the previous spring. The conspicuous vacuoles and lower epithelium may indicate a slightly more active condition in the male gland illustrated in Fig. 18. However, the general picture is one of colloid storage and quiescence.

Spawning smelt from South Bay, Ontario. In contrast to the colloid storage described in the spawning Miramichi smelt, the fish from South Bay have active glands. The follicular epithelium is cuboidal or high cuboidal. Some follicles are empty, many contain granular basophilic material (Fig. 22). Acidophilic refractile colloid, when present, is conspicuously eroded by peripheral vacuoles (Fig. 21).

DISCUSSION

Thyroids of juvenile alewives and smelt from the Atlantic coast are quiescent or mildly active at the time of seaward migration. They are similar to the glands of chum and pink salmon migrating to sea during their first spring and summer (Hoar and Bell, 1950). Although alewives and smelt do not have a prolonged freshwater feeding period and show a distinct smolt transformation, their seaward migration may extend over a period of several months. Thyroids are slightly more active in the later migrants. However, even the larger alewives, which are comparable in size to salmon smolt, do not have markedly active thyroids.

Thyroid stimulation seen in the sexually maturing alewives from the estuary and the colloid storage evident in thyroids of spawning and spent smelt from the Miramichi River correspond to conditions which have been previously described in Atlantic salmon at comparable times in their life cycle (Fontaine *et al.*, 1948). However, it should be noted that the detailed histological picture of the resting gland in spawning smelt differs from that of salmon (Hoar, 1939) and from the usual picture of thyroid involution (Ham, 1950). The high cuboidal or columnar epithelium, in contrast to the usual low cuboidal or squamous variety, is surprising. In spite of this irregularity, however, the glands are quiescent as evidenced by: (a) follicles packed with intensely eosinophilic homogeneous colloid, (b) absence of peripheral follicular vacuoles, and (c) lack of colloid in the lymphatics.

The most interesting findings in the present study arise from comparison of the coastal and landlocked fish. The thyroids of the landlocked fish are always more active than those of coastal fish in a comparable stage of development. Both juvenile and adult smelt were compared. Figs. 13 and 14 for juveniles and Figs. 19, 20, 21, and 22 for adults show the contrast. Only mature alewives were obtained from both environments. The marked difference is evident in Figs. 6 and 8. Further, this hypertrophy is so great in the case of the landlocked alewife that the gland has every appearance of exhaustion.

Heightened thyroid activity in anadromous fish from landlocked environments is not unexpected. As previously discussed, the elimination of water seems to require thyroid hormone and added osmotic stress may be expected when the anadromous fish is retained beyond the time of natural migration. The contrast between landlocked alewives and smelt is, however, particularly interesting. The alewife thyroid is enlarged, hyperplastic, and shows an exhaustion of colloid; the smelt thyroid is of normal size and, although active, contains an abundance of colloid. This contrast may depend upon different abilities in the two species to limit the amount of water in the tissues or to excrete water. At any rate, it is suggested that the alewife, owing to some difference in the biochemical constitution of its tissues, is under greater osmotic stress than the smelt. Another possibility, which should not be ignored, is a difference in the ability of the two species to utilize the relatively small amounts of iodine available in the Great Lakes region. Many years ago, Marine and Lenhart (1910) examined thyroids from a variety of Great Lakes fish (not including smelt or alewife) and found mildly active glands in several species. They concluded that fish, as well as man, may be affected by the supply of iodine in regions of endemic goiter. However, the mild activity described by Marine and Lenhart (1910) is no greater than the normal seasonal change shown by some fish (Hoar, 1939) or than that which precedes sexual maturation in several species (Fig. 5 and Fontaine *et al.*, 1948).

The relatively slow rate of growth in landlocked alewives may be related to the thyroid mechanism. Smelt reach essentially the same size in coastal and landlocked environments but alewives are much smaller when landlocked (Table I). The growth regulating function of the thyroid hormone is recognized. If the supply of hormone is inadequate for both osmotic regulation and growth the latter will probably be reduced. In man, inadequate supplies of hormone are known to produce dwarfing (cretinism) and experimental work suggests that a similar situation will occur in fish (Hoar, 1951).

Finally, it is suggested that the annual mortality of the Great Lakes alewives may be related to an exhausted thyroid. If, as has been argued, thyroid hormone is involved in the elimination of water, an exhaustion of the thyroid mechanism may lead to death from water intoxication. At least three factors may operate to increase the demand for thyroid hormone at the time of the annual mortality. Several species of fish normally show in the spring thyroid stimulation which is unrelated to sexual maturation (Hoar, 1939). Changes in illumination, acting by way of the pituitary, or temperature may be responsible but the exact mechanism has not been established. In addition, thyroid activity seems always to be associated with the early stages of sexual maturation and, finally, the seasonal elevation in water temperature may increase the osmotic load through a direct effect of temperature on permeability. This extra load of water will create additional demands for hormone. Any one of these factors may be sufficient to overload an already severely taxed thyroid mechanism.

SUMMARY

1. The cycle of thyroid activity found in Atlantic alewives and smelt is characteristic of anadromous fish which do not have a prolonged freshwater phase. Thyroids of seaward migrants are quiescent or mildly active. Maturing adults have active glands. Spawning adults show storage of colloid.

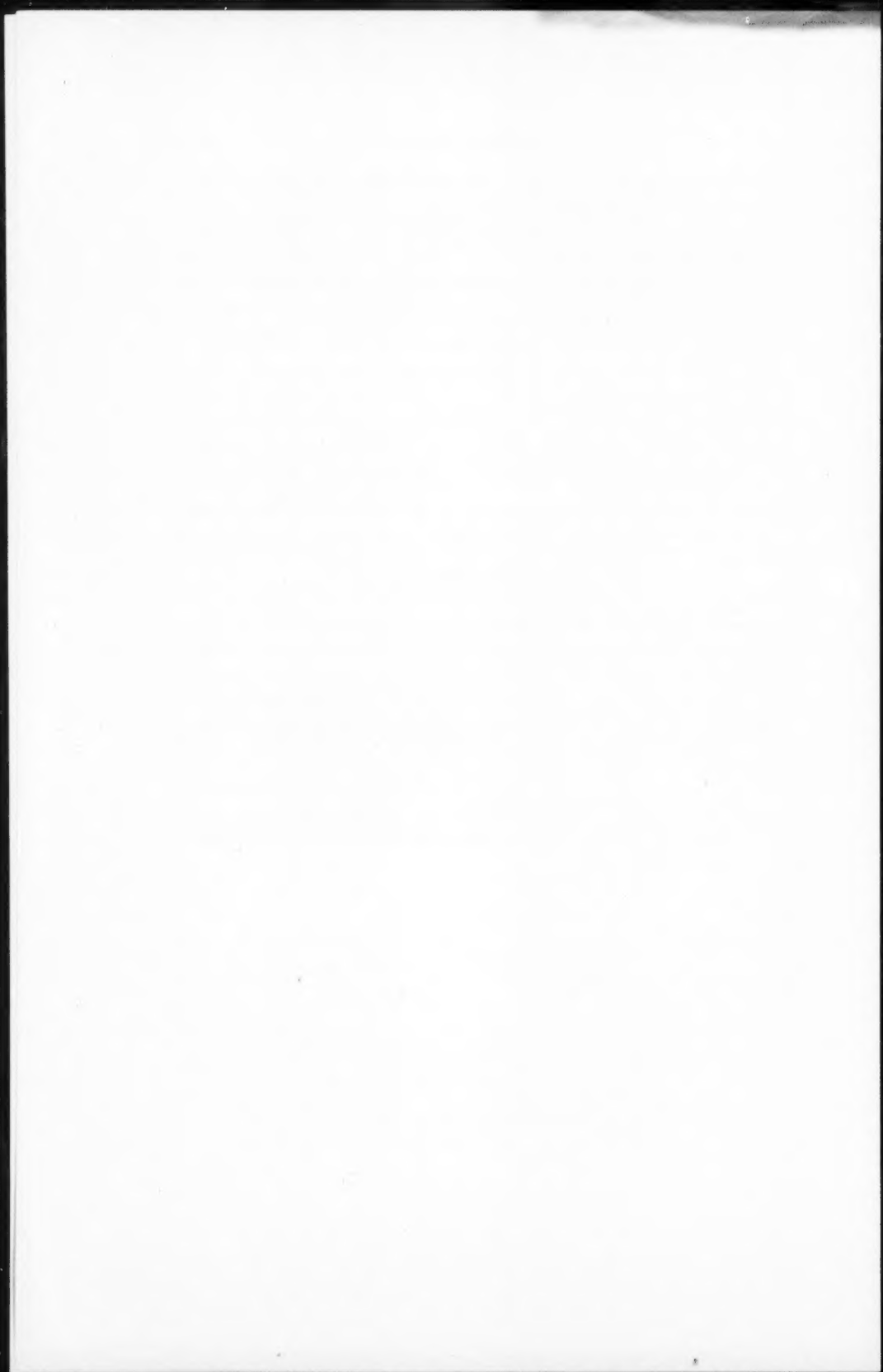
2. Thyroids of landlocked alewives and smelt are always more active than those of the same fish taken in coastal areas. In the smelt the gland is active but not hyperplastic; in the alewife it is extremely large, hyperplastic, and exhausted.

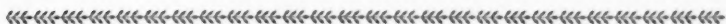
The relatively slow growth rate of the alewife and the periodic mortalities may be related to this condition of thyroid exhaustion.

REFERENCES

- CARL, G. C. and CLEMENS, W. A. (1948). The fresh-water fishes of British Columbia. Provincial Museum, Handbook no. 5. Victoria.
- DE ROBERTIS, E. (1949). Cytological and cytochemical bases of thyroid function. Ann. N.Y. Acad. Sci. **50**: 317-35.
- DYMOND, J. R. (1944). Spread of the smelt (*Osmerus mordax*) in the Canadian waters of the Great Lakes. Can. Field-Nat. **58**: 12-14.
- FONTAINE, M. (1948). Du rôle joué par les facteurs internes dans certaines migrations de poissons. J. Conseil **15**: 284-94.
- FONTAINE, M., LACHIVER, F., LELOUP, J. et OLIVEREAU, M. (1948). La fonction thyroïdienne du Saumon (*Salmo salar* L.) au cours de sa migration reproductrice. J. Physiol. (Paris). **40**: 182-4.

- FONTAINE, M. et LELOUP, J. (1950a). L'iodémie du jeune Saumon (*Salmo salar* L.) en eau douce. C.R. Acad. Sci. **231**: 169-71.
- (1950b). Sur l'iodémie de deux Téléostéens migrateurs Potamotoques *Salmo salar* L. et *Alosa alosa* L. au début de leur montée reproductrice. C.R. Acad. Sci. **230**: 775-7.
- GAYLORD, H. R. and MARSH, M. C. (1912). Carcinoma of the thyroid in the salmonoid fishes. Bull. U.S. Bur. Fish. **32**: 367-524.
- HAM, A. H. (1950). Histology. Philadelphia: Lippincott.
- HOAR, W. S. (1939). The thyroid gland of the Atlantic salmon. J. Morph. **65**: 257-95.
- (1951). Hormones in fish. Univ. Toronto Stud. Biol. 59, Pub. Ont. Fish Res. Lab. **71**: 1-51.
- HOAR, W. S. and BELL, G. M. (1950). The thyroid gland in relation to the seaward migration of Pacific salmon. Can. J. Res. **D28**: 126-36.
- LELOUP, J. (1948). Influence d'un abaissement de salinité sur la cuprémie de deux Téléostéens marins: *Muraena helena* L., *Labrus bergylla* Asc. C.R. Soc. Biol. (Paris) **142**: 178-9.
- LOVERN, J. A. (1934). Fat metabolism in fishes. V. The fat of the salmon in its young freshwater stages. Biochem. J. **28**: 1961-3.
- MARINE, D. and LENHART, C. H. (1910). On the occurrence of goitre (active thyroid hyperplasia) in fish. Johns Hopkins Hosp. Bull. **21**: 95-8.
- MCKENZIE, R. A. (1946). The smelt fishery of northeastern New Brunswick. Bull. Fish. Res. Bd. Can. **70**: 1-20.
- OLIVEREAU, M. (1948). Influence d'une diminution de salinité sur l'activité de la glande thyroïde de deux Téléostéens marins: *Muraena helena* L., *Labrus bergylla* Asc. C.R. Soc. Biol. (Paris) **142**: 176-7.
- PRITCHARD, A. L. (1929). The alewife (*Pomolobus pseudoharengus*) in Lake Ontario. Univ. Toronto Stud. Biol. 33, Pub. Ont. Fish. Res. Lab. **38**: 39-54.
- VAN OOSTEN, J. (1947). Mortality of smelt, *Osmerus mordax* (Mitchell), in Lakes Huron and Michigan during the fall and winter of 1942-1943. Trans. Amer. Fish. Soc. **74** (1944): 310-37.
- VLADYKOV, V. D. and MCKENZIE, R. A. (1935). The marine fishes of Nova Scotia. Proc. N.S. Inst. Sci. **19**, part 1: 17-113.
- WILDER, D. G. (1947). A comparative study of the Atlantic salmon, *Salmo salar* Linnaeus, and the lake salmon, *Salmo salar sebago* (Girard). Can. J. Res. **D25**: 175-89.





"Even-year" and "Odd-year" Pink Salmon Populations

FERRIS NEAVE

Presented by J. L. HART, F.R.S.C.

SINCE pink salmon (*Oncorhynchus gorbuscha*), to the best of our current knowledge, invariably mature and die at the end of the second year of life, it has long been recognized that the adult runs appearing in any two consecutive years represent entirely separate populations of the species. Since these stocks for the most part occupy the same regions and spawn in the same watercourses, special opportunities are provided for comparing the status and fortunes of two populations possessing similar constitutional and geographic opportunities but entirely prevented from interbreeding.

Particular interest attaches to well-known cases in which the disparity in abundance between the stocks is so great that years of immensely productive fishing alternate regularly with years which yield insignificant returns from the same waters.

This situation has sometimes led to the belief that the existence of a very large stock in one series tends to suppress the population of the other series—a view which has been more fully developed in relation to a somewhat similar phenomenon of "dominance" exhibited by the sockeye (*O. nerka*) populations of the Fraser River watershed (Ricker, 1950).

Whether or not the causes of population disparity in pink salmon can be immediately elucidated, a decision about the independence or otherwise of each population with respect to the other would in itself be helpful to the conservationist. If it were shown that the existence of two large populations in the same waters is biologically incongruous, fisheries management would have to work within the limitations of this framework. If on the other hand there is no fundamental incompatibility, efforts can be directed towards discovering and removing the causes of weak stocks.

In evaluating the evidence bearing on this problem it is pertinent to survey the available information concerning the geographic status of pink salmon belonging to the two great branches of the species, that is, fish maturing in "even" years and fish maturing in "odd" years. For

convenience, these two kinds of pink salmon are designated herein as "E fish" and "O fish".

RELATIVE ABUNDANCE OF E- AND O- PINK SALMON

1. In British Columbia

Past records of the abundance of adult pink salmon (that is, "catches" and "escapements") for the numerous administrative areas of the British Columbia coast cannot be regarded as accurate in an absolute sense. They are undoubtedly adequate, however, to show the direction of major changes in abundance from year to year or to reveal marked discrepancies between a series of even years and a series of odd years.

Table I presents certain such estimates of catches for areas of the northern and central coastal regions of British Columbia. These areas

TABLE I
RELATIVE ABUNDANCE OF E AND O PINK SALMON, IN NORTHERN B.C.,
AS INDICATED BY REPORTED ANNUAL CATCHES

Area	Period	Average catch (wt.)		Ratio E:O
		E	O	
North Queen Charlotte Is.	1930-1949	45,994	224	205:1
South Queen Charlotte Is.	1934-1949	14,901	1,381	11:1
Nass River	1930-1949	39,183	20,323	1.9:1
Skeena	1930-1949	51,313	47,933	1.1:1
Grenville-Principe	1930-1949	31,715	13,629	2.3:1
Butedale	1930-1949	59,192	39,430	1.5:1
Bella Bella	1930-1949	17,780	35,780	1:2
Bella Coola	1930-1949	22,538	37,985	1:1.7
Rivers, Smith Inlets	1930-1949	5,008	8,601	1:1.7

TABLE II
RELATIVE ABUNDANCE OF E AND O PINK SALMON IN SOUTHERN B.C.,
AS INDICATED BY REPORTED ANNUAL ESCAPEMENTS*

Area	Period	Average escapement (1000 ⁰)		Ratio E:O
		E	O	
Quathiaski	1934-1949	213.8	109.5	2:1
Comox	1934-1949	110.4	165.0	1:1.5
Toba Inlet	1934-1949	11.8	117.1	1:9.9
Jervis Inlet	1934-1949	58.1	167.4	1:2.9
Nanaimo	1934-1949	4.0	5.3	1:1.3
Clayoquot	1934-1950	2.8	1.9	1.5:1
Quatsino	1935-1946	167.0	3.8	44:1
Sooke Trap catch*	1938-1949	.474	126.3	1:266

*The Sooke Trap catch is included as being the best available indicator of the ratio between E and O fish travelling to Puget Sound and the Fraser River.

are defined in Fig. 1. For the southern portions of the coastline, catch figures cannot readily be used as an indication of the condition of the stocks "belonging" to individual areas, since many of the fish caught

are transients migrating to other destinations. In particular, the large biennial runs to the Fraser River and Puget Sound pass through and influence the catches of many other fishing areas. For these areas, therefore, comparisons have been made (in Table II) on the basis of reported escapements to the spawning streams. Because of the difficulties involved in making estimates of spawning populations in a vast number of streams of different size and character, these figures are



FIGURE 1.—Coastal regions of British Columbia, showing areas referred to in text. Stippling (Queen Charlottes) represents area in which streams show no extreme disparity (see text).

presented only for the purpose of demonstrating the gross features discussed below. Actually, estimates are commonly made as categories, for example "between 2,000 and 5,000"; "between 50,000 and 100,000." The figures used have been arrived at by taking the midpoints of the various categories.

Reviewing the 17 areas represented in Tables I and II, it is at once evident that two of them show an extreme degree of disparity between

E and O fish, the north Queen Charlottes having an overwhelming preponderance of E pinks and the Fraser-Puget Sound runs an equally impressive dominance in the O stocks. A third area (Quatsino) shows a pronounced but less extreme disparity favouring the E population. In all other areas the difference, for the periods quoted, is of a much lower order. Although the maintenance for several generations of a two- or three-fold difference in the magnitude of E and O catches sometimes leads in common parlance to the recognition of alternate "off" years and "on" years, the leading position not infrequently changes from one stock to the other (see Figs. 3 and 4). For nearly all of the areas listed in Tables I and II a shorter period of years could be selected which would reverse the preponderance suggested by the ratios given in these tables.

Since each of the areas referred to possesses numerous salmon streams, it would theoretically be quite possible for this general condition of near-equality of the stocks to represent merely the combined output of numerous spawning grounds which, taken individually, might show great disparity between E and O stocks. If E and O fish tended to spawn in different streams, an underlying similarity between the phenomenon observed in the Fraser and Queen Charlotte areas and the situation existing elsewhere could be established.

Observations made by personnel of the Fisheries Research Board and the much more comprehensive surveys of the Department of Fisheries show, however, that there is no such segregation of the breeding places of the two stocks. An examination of Departmental records shows clearly that in general the individual streams reflect closely the ratios shown by the commercial catches in the sea. The writer has seen reports relating to more than 200 pink salmon streams in the "sub-equality" areas of British Columbia, each stream being covered for a period of from 7 to 17 years. In no single instance has he found evidence of a degree of disparity between stocks which is at variance with the general picture obtained from the consideration of large areas. In most cases an overlap is indicated in the abundance of fish belonging to E and O populations.

A few specific examples may be cited from many streams showing a very high order of abundance in both odd and even years. The writer is personally familiar with the streams mentioned.

The Neekas River, in the Milbanke Sound area, has an accessible length of about one mile and an average width of about 20 yards. It supports large runs of both pink and chum (*O. keta*) salmon and the spawning grounds appear to be fully occupied by the presence at any given time of 40,000 salmon. Between 1935 and 1945 estimates of pink

salmon alone were of the order of 75,000 or higher in four even years and five odd years.

Evelyn Creek, on Hawkesbury Island, is a very small stream, about one and a half miles long. The flow on September 1, 1945, at the time when the adult fish were beginning to enter, was estimated to be only 6 c.f.s. (this was undoubtedly an unusually low level). Escapements of between 50,000 and 100,000 pink salmon were assigned to this stream in 1942, 1943 and 1945. The assumption of errors up to several hundred per cent would not alter the conclusion that full utilization of available spawning ground was being made by both E and O fish.

The Koeve River, flowing into Fitzhugh Sound, is well known to fishermen and Departmental officers as a large and constant contributor to the catches of the Queen Charlotte Sound area. It is a somewhat larger stream than those previously mentioned but the favourable spawning areas probably do not total more than three miles in length. Both even- and odd-year escapements are commonly estimated as "over 100,000." For recent years of both series this is believed to be a very conservative statement.

While they do not change the general impressions formed from an examination of catch figures, stream reports do, however, enable us to define more precisely the boundaries of the Queen Charlotte Island region which is characterized by extreme disparity. From Table I it would appear that only the northern portion of Graham Island displays this condition in an acute form, the rest of the island group showing only a moderate degree of E dominance. Departmental records make it clear that in fact most of the pink salmon streams of both Graham and Moresby Islands have virtually no runs in the odd years. A few rivers, however, located in a belt which extends on both sides of Skidegate Channel, have good or fair runs in both even and odd years and in fact show almost precisely the same state of affairs as the streams of the opposite (mainland) coast of Hecate Strait (see Fig. 1). Streams which can be named as belonging in this category are: Tlell River, flowing to the east coast of Graham Island; Riley Creek, flowing to the west coast of Graham Island; Copper River, flowing to the east coast of Moresby Island; Deena River, flowing to the north coast of Moresby Island (Skidegate Channel).

As regards the freshwater situation, therefore, most of Graham and Moresby Islands can be designated as a region of extreme E and O disparity, with a small central area which transects this region and which shows a condition characteristic of most other parts of the British Columbia coast.

In the southern mainland region the writer knows of no streams

which provide exceptions to the thoroughgoing dominance exhibited by the O fish, although the abundance of these varies considerably in different generations. E fish, however, are not entirely absent, having been reported in small numbers in many of the same watercourses. The disparity is not confined to the Fraser River watershed, being characteristic of streams in the adjacent districts of Puget Sound and Howe Sound. It does not extend to the southern end of Vancouver Island nor to the streams of Jervis Inlet.

The existing conditions with respect to the relative abundance of E and O fish in British Columbia as a whole can be summarized as follows:

1. Throughout the greater part of the range of the species within or near the province, a long-term condition of near-equality exists, with either stock capable of showing greater abundance in certain years or periods.

2. Throughout the periods for which records are available, local conditions of extreme disparity have prevailed in the Queen Charlotte Islands and in the southern mainland area. A less extreme disparity has existed in the Quatsino area of northwest Vancouver Island.

3. The ratios between E and O fish are characteristic of *regions* and are not the exclusive property of individual streams. Even the apparently mixed situation on the Queen Charlotte Islands appears to partake of this regional nature.

2. In Other Regions

The total geographic range of the pink salmon, excluding sparse or infrequent occurrences in Oregon and California, extends from the state of Washington northward along the American coast to northern Alaska and the Mackenzie River. On the Asiatic side of the Pacific it ranges southward as far as northern Korea and northern Honshu. Such data as the writer has seen relating to the comparative abundance of E and O fish throughout the greater part of this vast realm are mainly in the form of catch records for very large districts within which there is an obvious possibility of diverse local conditions. Nevertheless, even general information from the much greater territories occupied by pink salmon elsewhere is helpful in assessing the problem of disparity as witnessed in British Columbia.

The following remarks concerning Alaska are based on the annual catch figures supplied by the U.S. Fish and Wildlife Service and the canned packs reported in the *Pacific Fisherman Yearbook*. During the last fifteen or twenty years each of the seven recognized statistical districts of southeast Alaska shows much overlapping in the quantities reported for even and odd years. The total range of variation tends to

be of a similar order for both stocks and their relative abundance can be said to be in general accord with the condition which prevails along the greater part of the British Columbia coast. The same may be said of the five districts of central Alaska (comprising the region from Cape Spencer to the Alaska Peninsula) for which pink salmon packs are reported (in Cook Inlet the E fish are considerably more numerous on balance but there is no disparity of the extreme and persistent type to which reference has been made). In western Alaska (Bristol Bay, Yukon, etc.) certain series of figures give the impression of a thorough-going disparity favouring the E fish. The record is not consistent in this respect, however, and, since pink salmon catches are always relatively small in this region, it seems unsafe to draw definite conclusions regarding the ratio of the populations.

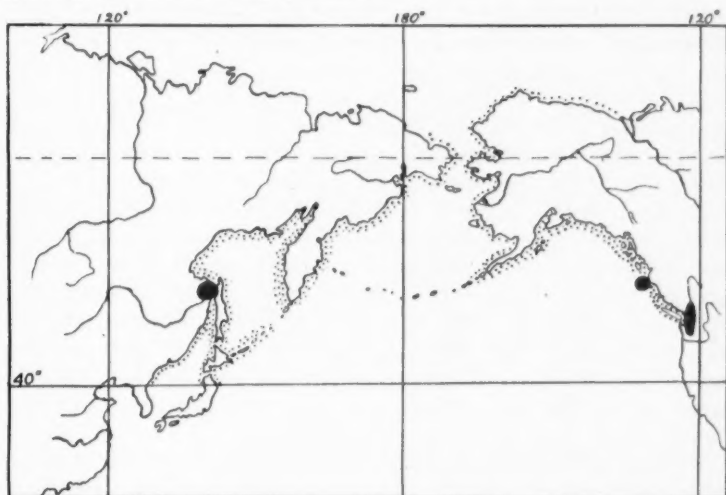


FIGURE 2.—North Pacific region, showing general distribution of pink salmon and (in black) areas of extreme disparity.

On the Asiatic side Pravdin (1940) quotes catch figures for the years 1926 to 1934 inclusive for each of 10 regions of the U.S.S.R. coast. From south to north these are: Primor; Nikolaevsk; Sakhalin; Okhotsk; Gijiginsk; Ichinsk; West Kamchatka; East Kamchatka; Karagin; Olyutoro-Navarin. The figures given show some degree of overlapping between E and O fish for six of these districts (in the two northernmost sections the leading position appears to have swung from the E to the O stock within the period). In the four regions for which no overlap is

indicated, the ratio is nevertheless quite low (7.5:1 or less) in two cases. Of the two remaining districts one, Gijiginsk, appears to be a relatively unimportant producer of pink salmon. The ratio obtained from Pravdin's figures is 31:1 in favour of the E stock—or roughly the condition prevailing in the Quatsino Sound area of British Columbia. The other exception is Nikolaevsk, which includes the very important fisheries at the mouth of the great Amur River. Here, the indicated disparity is even more extreme than that of the Fraser River area—but in favour of the E stocks. A further parallel can be seen in that the condition apparently does not extend to Sakhalin Island, the geographic relationship of which to the Amur is rather like that of Vancouver Island to the Fraser. Of especial interest, however, is the information supplied by Berg (1928) that the condition in the Amur district is of recent origin. Berg's figures for pink salmon caught annually near the mouth of the Amur are as follows (in thousands of individuals).

Odd Years		Even Years	
<i>Year</i>	<i>Number</i>	<i>Year</i>	<i>Number</i>
1907	1,478	1908	4,600
1909	2,950	1910	7,701
1911	3,856	1912	7,528
1913	7,469	1914	14,528
1915	994	1916	9,243
1917	557	1918	14,876
1919	420	1920	12,000
1921	200	1922	9,000
1923	18	1924	12,217
1925	0		

Pravdin's later data are given by weight. The following figures represent "thousands of centners" (a rough calculation on the basis of an average weight of 4 lb. per individual fish would give 27.5 fish per centner (= 50 kg.) and indicates that the 1926 catch was down to less than 5,000,000 fish).

Odd Years		Even Years	
<i>Year</i>	<i>Weight</i>	<i>Year</i>	<i>Weight</i>
		1926	171.5
1927	0	1928	116.5
1929	0	1930	73.2
1931	0.3	1932	75.49
1933	0.39	1934	53.4

The implications are that a very moderate preponderance of E fish became exaggerated by a slump which appeared in the offspring of the 1913 run. The decline in O fish continued for the next five generations by which time commercial production was nil. During this time the E fish continued to maintain themselves at a high level. Pravdin's figures for the ensuing nine years indicate that the catches of E fish declined during this period but with little revival of the O stocks.

This brief review of conditions obtaining in other parts of the geographic range of the species tends to confirm the impressions formed from a consideration of British Columbia data alone, namely, that a state of semi-equality of E and O stocks is usual and that extreme disparity, while it occurs in widely separated areas, is local and infrequent.

CHANGES IN ABUNDANCE OF E AND O STOCKS

Figs. 3 and 4 show reported catches for various areas of the northern and central British Columbia coast over a period of approximately 20 years. Although, as stated previously, precise quantitative accuracy is not claimed for these records, the writer is confident that the direction of major changes in abundance is in general disclosed by these graphs.

Certain consistencies are apparent. In all areas except the north Queen Charlottes, where the O runs are practically nonexistent, each stock occupies a leading position at some time during the period shown. While changes in one stock appear to be independent of changes in the other stock, the direction of change in a given year is frequently similar in many areas. Thus, the E catches show a marked decline in all areas in 1932. Other even-year declines are apparent in nearly all areas in 1940 and 1946. Marked gains were registered in all areas south of the Skeena in 1944 and in all areas in 1948. The odd-year fish showed a decline in all areas except the Skeena in 1935 and heavy declines in all areas in 1941 and 1947. A widespread increase was shown in 1933; in 1939 all areas showed gains; in 1943 a very heavy increase occurred in all areas south of the Skeena, and in 1949 there was a substantial improvement everywhere.

These common tendencies suggest strongly that changes in abundance are frequently determined by factors which operate over relatively large regions.

DISCUSSION

Reference is made again to the question how or why two populations with similar requirements and opportunities can continue to inhabit the same area on a totally different scale of numerical abundance.

The view that the smaller population is held down to a low level by

the existence of the larger population may be considered first. Certain points which appear to favour this view are:

1. Great disparity in the stocks of pink salmon is characteristic of the Fraser River system, where the "dominance" of certain sockeye stocks has also been conspicuous. The disparity in the latter species has

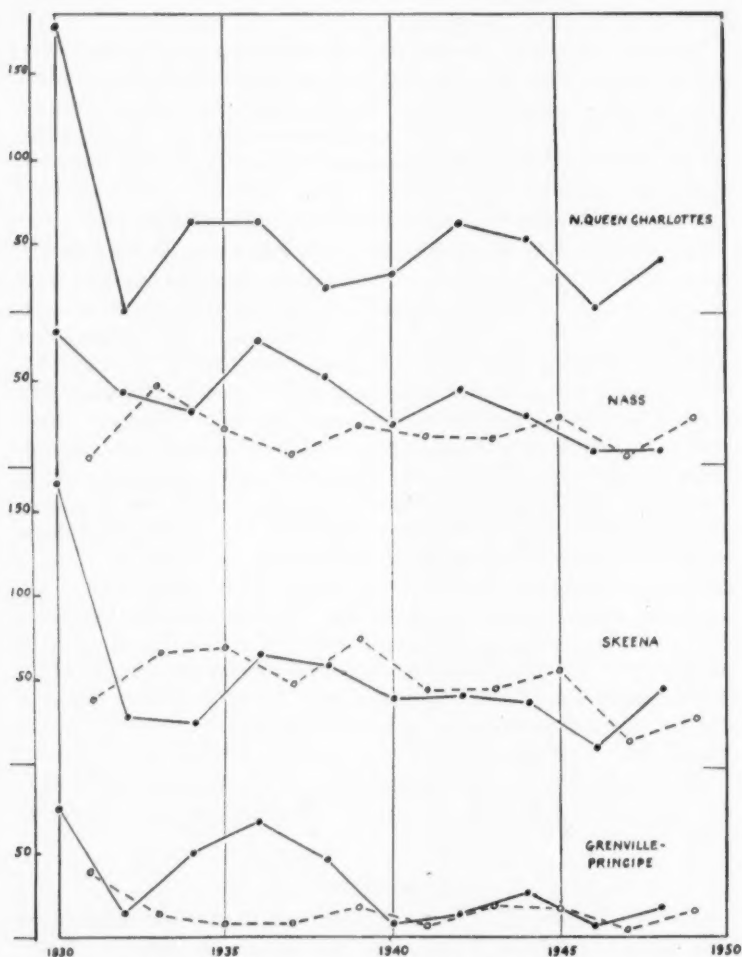


FIGURE 3.—Reported annual catches (thousands of cwt.) of pink salmon in areas of northern British Columbia. Solid line—E fish. Broken line—O fish.

been thought to be due to interaction between year-classes (Ricker, 1950) and it seems reasonable to seek a common explanation for the two species.

2. Attempts to establish "off-year" pink salmon runs in a stream possessing an abundant population of the other stock have been unsuccessful (Pritchard, 1938).

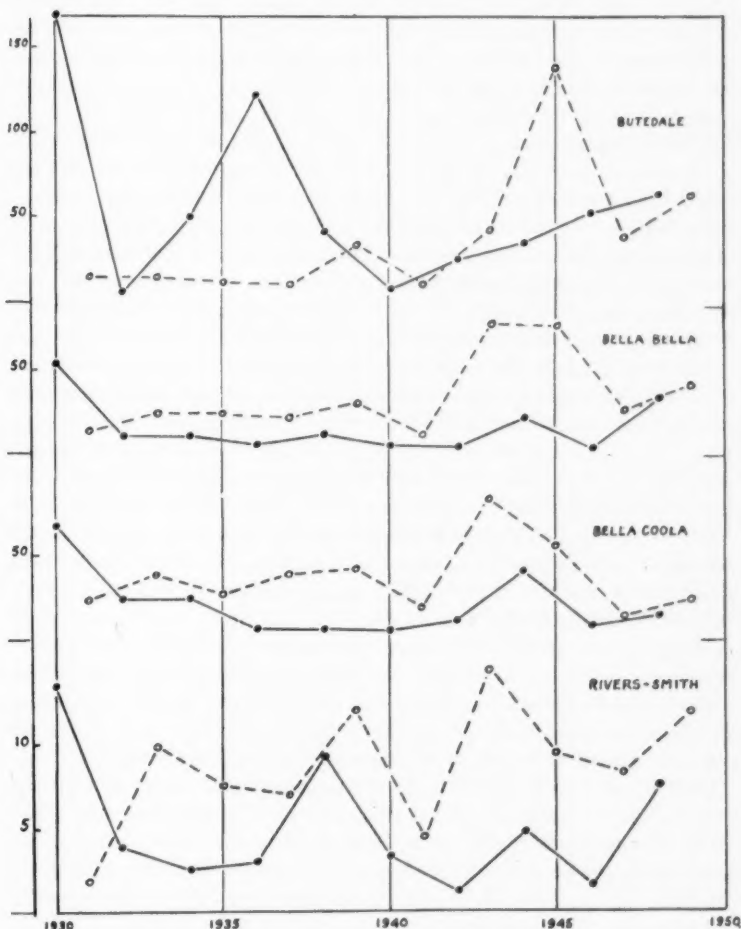


FIGURE 4.—Reported annual catches (thousands of cwt.) of pink salmon in areas of central British Columbia. Solid line—E fish. Broken line—O fish.

3. In the only documented instance of the inception of a state of extreme disparity in pink salmon (Amur River, see above), the decline of one population apparently synchronized with an increase in the other population.

Before presenting arguments which oppose this view, it may be pointed out that when two populations continue to exist at their respective levels (as seems, broadly speaking, to be the case in the Fraser system) each is being equally successful in reproducing itself. The smaller population is only being "held down" (relative to the larger one) if it is assumed that the higher population represents a more "natural" state to which the smaller stock should be approximating. The large population could in fact only be "holding down" the small one to its own reproductive rate. If, on the other hand, there are factors which tend to keep populations at or near their existing levels, continued disparity requires only an initial cause to keep it in being. In any case, it would seem that *production* of disparity is a different matter from its maintenance, since the former requires that the survival rates of the stocks be different whereas the latter requires that they be the same—that is, unless one stock is totally absent.

The view that the abundance of one stock inhibits the abundance of the other stock does not seem to be supported by the general geographic evidence already cited. Extreme disparity is exceptional (see Fig. 2). There are many regions, including such centres of abundance as south-east Alaska and central British Columbia, in which both stocks can show very high levels of population size. There is no evidence of a general reciprocal relationship between the size of E and O stocks. It is possible to cite examples which seem directly opposed to such an idea. For instance, the rise of the O stock to an extremely high level in 1943 in the Bella Bella, Bella Coola, and Rivers Inlet areas was followed by a marked increase in the E stocks of these areas in 1944 (Fig. 4). In the previously cited case of the establishment of a strong disparity in the Amur district, the initial decline of the O fish does indeed appear to have synchronized with an increase in the E stock. But if the available catch figures are accepted as indicative of the condition of the runs, the E population then remained nearly constant for a series of generations, whereas the O stock continued to dwindle with each successive life-cycle. The subsequent decline of the E stock in the years 1926 to 1934 seems to have elicited no such marked or rapid revival of the O fish as might be expected if this were the factor which was holding them down.

If, however, it is conceded that the general evidence concerning the independence of the two stocks is insufficient to exclude the possibility of interaction as a cause of continued disparity, it is necessary to con-

sider the periods in the life-cycle when such interaction might occur. In the case of the sockeye an explanation has been sought in terms of intraspecific competition or intraspecific predation during the rather lengthy period of lake residence. Since no such period occurs during the life-history of the pink salmon, no similar hypothesis can be set up for this species. There is in fact no overlapping between stocks at any stage of freshwater existence, and the only possibility of interaction in this medium would seem to lie in one stock rendering the habitat unsuitable in some way for the population of the following year. This possibility can be discounted in view of the very heavy pink salmon populations which do in fact occupy the same stream areas year after year in many parts of the geographic range of the species. Specific examples in British Columbia have been cited previously.

While evidence has been presented elsewhere (Davidson and Hutchinson, 1943; Neave, 1952) that pink salmon abundance tends to be determined by freshwater factors, the possibility that the condition of extreme disparity is maintained by interaction between E and O stocks in the ocean remains to be considered. On general grounds it seems rather unlikely that successive year-classes can establish such exclusive interrelations that they can determine their relative abundance without reference to the vast and varying numbers of other predators or competitors in the unrestricted environment of the sea. Other objections can also be raised.

Underyearling pink salmon, which from their numbers, distribution, and greater abundance in even years undoubtedly include many Fraser River fish, are to be found in the Strait of Georgia and among the San Juan Islands until July and early August (Foskett, 1951; Clemens, 1952). The fish of the other stock by this time have nearly completed their marine feeding period and are on their return journey to fresh water. They are concurrently contributing to the commercial fishery on the southwest and north coasts of Vancouver Island. If the same routes and depths are followed, the outward and inward migrations must be in close relation at some period, but it may be seriously doubted whether there is any prolonged feeding in common areas by different year-classes of fish which migrate extensively during such a relatively short period of marine life.

The view that continued disparity is the result of competition or predation between E and O populations seems to lead to the inference that in areas where both are abundant the stocks are not in contact at the appropriate period. The writer finds it difficult to think that there are a few special areas scattered within the wide range of the species wherein such contacts have been able to produce a continued eclipse of one stock

whereas in other areas the abundance of both seems entirely compatible. The difficulty becomes acute in the case of the Queen Charlotte Islands. Here it would have to be supposed that the marine phases of the O fish of a few streams are insulated from a form of predation or competition which imposes a continuous depression on the fish derived from nearby streams on all sides of them.

In seeking an alternative explanation for the occurrence of extreme and persistent disparity, the possibility might be considered that one stock has never been able to establish itself in certain areas. The apparently complete dichotomy of the species into E and O stocks is presumably a relatively recent event. The geographic areas suitable for pink salmon must have changed considerably during postglacial times. Once segregation into the two groups had been effected, colonization would be a separate process in each case and would not necessarily proceed at the same rates in all regions. The Queen Charlotte Islands might well present a difficult area for colonization from the mainland by a species with pronounced homing tendencies. The small area on these islands which is occupied by appreciable numbers of O fish might be interpreted as the bridgehead of an invasion which is now in progress. In the Fraser-Puget Sound area, which lies at or near the southern limit of the present distributional range, it might be argued that the E fish have arrived too recently to have encountered the specially favourable conditions necessary for a great expansion of population.

Such a theory would not account for the recently achieved disparity of the Amur River district. It must therefore be concluded that some and perhaps all cases of extreme disparity have been initiated by a different survival rate between stocks which were formerly on a more equal footing. As already pointed out, this different survival rate could not have persisted in cases where the two stocks are maintaining their relative positions and might indeed have been a very brief phenomenon.

In connection with Figs. 3 and 4, it has been noted that changes in abundance of pink salmon from one generation to the next are regional in their application. This is true also of the occurrence of extreme disparity. The latter may reasonably be thought to have been initiated by factors similar to those which induce the variations commonly seen in pink salmon stocks. These variations have been related to meteorological conditions affecting the freshwater phases of the life-history (Davidson and Hutchinson, 1943; Neave and Wickett, 1949; Neave, 1952). Such conditions can be regional in effect, and in a given year would affect only one stock. Factors which could adversely affect one stock in a regional manner include: droughts; heavy floods; unfavourable water temperatures; exposure and freezing of spawning grounds.

Increased survival is promoted by the maintenance of relatively constant water levels and favourable temperatures during the freshwater period. A mechanism evidently exists for initiating a difference in abundance between the E and O stocks.

Regarding the further development and fixation of disparity, the writer (Neave, 1952) has emphasized elsewhere the existence of factors which tend to confirm and exaggerate changes in population size, as well as factors which tend to promote stability. Attention was especially directed to the probable effect of predators during the migration of salmon fry to the sea, in inflicting relatively heavier losses on smaller populations. When a population exceeds or falls below certain limits of size it is likely to be subject to influences which tend to maintain the direction of change or at least to oppose a return to the former level.

The Amur data suggest that a disaster attending the reproduction of the 1913 spawning stock depressed the 1915 population to a point well below the levels recorded in previous generations. From this point the decline continued in each generation, resulting in commercial extinction in 1925 (of the escapement in that year Berg says "there were only single specimens that ascended small rivers falling into the Amur below Nikolayevsk"). The other stock maintained itself well during this period. It can hardly be supposed that good and bad reproductive seasons alternated regularly for 12 years. We must accordingly conclude that the initial catastrophe brought its own train of subsequent events. Conceivably, disparity could also result from an *increase* of one stock. Given an exceptionally favourable reproductive season, a population might "break through" the existing predator control and attain a relatively permanent high level of abundance. To attain extreme disparity in this way, however, the process would have to start from a relatively low level of the stocks, since limitations of habitat other than predators would certainly stop expansion at some point.

It is not necessary to assume that a major downward change inevitably proceeds to the extreme degree shown in the case of the Amur. Stabilization might occur at some relatively low level at which the young fish begin to be less available to predators and the reproductive efficiency of the population is higher than that of a large population. The evidence indicates that pink salmon populations can be stabilized (relatively speaking) at various levels, at least when in different localities. The Amur case does suggest strongly, however, that between a high status and a low status there may be intermediate levels of abundance which are very difficult to maintain under natural conditions. In cases where disparity has become acute, chances of a small population attaining the status of the large one may be very small.

Extreme, persistent disparity is a rare condition in pink salmon. Apparently the limits within which the populations can change without being definitely committed to a new status are broad enough to permit very considerable fluctuations and are only transcended under highly exceptional and infrequent circumstances.

Those who are interested in the practical problem of promoting large pink salmon runs in "off" years should consider the possibility that a gradual increase of the existing stocks or the planting of a few hundred thousand eggs to start a new population may frequently not be a feasible approach to the problem unless supplementary measures are taken. On the other hand they can derive satisfaction from the observed fact that large as well as small or negligible populations can exist in many waters, and from the evidence that the two states are not reciprocal. Present knowledge suggests that the change from a low to a high status should be made as far as possible in one "jump," or that the factors (believed to be especially the removal of fry-migrants by predators) hindering a more gradual increase should be eliminated.

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REFERENCES

- Alaska fishery and fur seal industries. U.S. Fish & Wildlife Service, Washington, D.C.
- BERG, L. S. (1928). The Pacific Research and Fishery Station at Vladivostok. Proc. 3rd Pan-Pac. Sci. Congress, 2239-40.
- CLEMENS, W. A. (1952). On the migration of Pacific salmon (*Oncorhynchus*). Trans. Roy. Soc. Canada, 3rd ser., 45 (sec. V): 9-17.
- DAVIDSON, F. A. and HUTCHINSON, S. J. (1943). Weather as an index to the abundance of pink salmon. Pac. Fisherman, May 1943.
- FOSKETT, D. R. (1951). Young salmon in the Nanaimo area. Prog. Repts. Pac. Coast Stations, 86:18-19.
- NEAVE, F. Principles affecting the size of pink and chum salmon populations in British Columbia. J. Fish. Res. Bd. Canada (in press).
- NEAVE, F. and WICKETT, W. P. (1949). Factors affecting the freshwater development of Pacific salmon in British Columbia. MS., Pac. Sci. Congress.
- Pacific Fisherman Yearbook. Seattle.
- PRAVDIN, I. F. (1940). (Investigations of far eastern salmon.) Bull. Pac. Sci. Inst. Fish. and Oceanog., 18:1-107.
- PRITCHARD, A. L. (1938). Transplantation of pink salmon (*Oncorhynchus gorbuscha*) into Masset Inlet, B.C., in the barren years. J. Fish. Res. Bd. Canada, 4:141-150.
- RICKER, W. E. (1950). Cycle dominance among the Fraser sockeye. Ecology, 31:6-26.

